The American
Midland Naturalist

Devoted to Natural History, Primarily
that of the Prairie States

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THE TRANSITION FROM ROOT TO STEM IN HELIAN-
THUS ANNUUS L. AND ARCTIUM MINUS BERNH.

MARGARET BENEDICT SILER

I. INTRODUCTORY

A. HISTORICAL

The earlier investigators of root-stem transition used successive hand sections of seedlings, and their work culminated in 1891 in the development of a diagrammatic representation of transition phenomena by Philippe Van Tieghem's system of three types of transition (31). A fourth type of transition found in certain monocots was added by Miss Ethel Sargant in 1900 (23). Diagrams of these four types may be seen in Eames and McDaniels' "An Introduction to Plant Anatomy" (11, p. 243). This system of representing the structural transition from root to stem, or vice versa, through the hypocotyl, is valuable as a short-hand method of describing what one sees in a series of sections through a given seedling. The disadvantage of this method lies in the fact that one does not gain from this system an adequate picture of the transition from root to stem.

The very word "transition" implies a moving and a change. In Van Tieghem's types this movement and change in position of parts is visualized as a splitting and fusion of xylem and phloem groups and rotation of protoxylem from an exarch to an endarch position. The mature xylem and phloem groups do not actually split, rotate, and fuse. Such appearances are

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due to the manner in which these tissues mature.   Unless a theory and exposition take into account the actual progressive development of tissues as well as the resulting arrangement, the transition is not properly understood.   T. G. Hill and Miss Ethel De Fraine in their work on seedling anatomy have stressed the physiological factor in the development of root, hypocotyl, and cotyledonary structures (18).   M. Gustave Chauveaud in his memorable work on the conducting appara- tus of plants has given us a description of transition in which the development of vascular tissue is traced from a similar primitive condition in radicle, hypocotyl, and cotyledons to the structures characteristic of these parts at maturity (4).

The earliest workers on seedling anatomy and the transi- tion from root to stem included Clos (5), Gérard (14), Vuil- lemin (32), Dangeard (8), and Van Tieghem (31), and from their work we derive the three types established by Van Tieghem.   Later, English botanists seized upon the subject of seedling anatomy as a possible field for phylogenetic work. Miss Sargant developed a theory of the origin of monocots from dicots by the fusion of the two cotyledons accompanied by the development of the geophilous habit (24).   This theory was based on the occurrence of the monocot *Anemarrhena* type of transition [her fourth type (23)], in certain *Ranun- culaceae.*   Later work by Miss De Fraine (10) and by E. Lee (20) have weakened the value of such evidence and removed the basis for the theory.   R. H. Compton (6), based on his work on the *Leguminosae*, has given us the additional idea that seedling anatomy is intimately related to the size of the seedling.

Within the past few years the first American work was carried out by Sr. Raphaelis Gehlen on two legumes (13). Her seedlings were possibly too old as the plumular traces were well developed.   Sr. Raphaelis says that "Eames and McDaniels have arranged a series of diagrammatic drawings showing how the 'forking, rotation and fusion of strands' in various types of plants take place."   These authors (11) have produced a good series of diagrams of Van Tieghem's three

types and of Miss Sargant's fourth type, which they have renamed "types A. B. C. D". Sr. Raphaelis compares the transition in the seedlings which she studied to type "A" as given by Eames and McDaniels instead of to the original Van Tieghem Type I. Other work on transition by American authors (2, 19) has included the subject only incidentally.

This study of root-stem transition in certain *Compositae* was undertaken at the suggestion of Dr. J. Hobart Hoskins.

B. ROOT-STEM TRANSITION IN THE COMPOSITAE

One of the earliest descriptions of the transition from root to stem in *Compositae* is found in R. Gérard's "Recherches sur le passage de la racine à la tige" of 1881 (14). In this paper *Carthamus tinctorius* L. and *Tagetes erecta* L. are described most accurately in regard to internal anatomy. Gérard describes the same arrangement of xylem and phloem later described by Gustave Chauveaud. Gérard does not interpret this arrangement, but merely describes the passage from root to stem.

In 1911 Chauveaud (4) reported his investigations on fifteen species of *Compositae*, including: *Silybum Marianum* (L.) Gaertn., *Tagetes lucida* Cav., *Dahlia coccinea* Cav., *Helianthus annuus* L., *Vernonia arkansana* DC., *Cichorium amara*, *Carthamus tinctorius* L., etc. In these Composites he traced the development of two types, those characterized by a diarch, and those characterized by a tetrarch root structure.

In 1914, E. Lee published an extensive study of the *Compositae* (21), including about fifty species. All of the seedlings have either diarch or tetrarch root structure. Lee correlates the type of transition with the type of cotyledon venation, but says that there is really only one type of transition with the tetrarch and diarch root situations as extremes of a series. He concludes as have Hill (16), De Fraine (10), and others that seedling structure is not a basis for determining plant affinities.

C. METHOD USED IN THE PRESENT WORK

In this study it is planned to trace a series of sections through seedlings of different ages, and then to trace a series of sections at comparative levels in successively older seedlings. The combination of the two series is the method followed by Chauveaud (4). By this procedure it is possible to present Chauveaud's interpretation of the root-stem transition which has not yet been followed by English workers. Also a more diagrammatic representation will be made of the transition phenomena in a single plant as Lee (21) and others have done.

II. STUDY OF THE SEEDLINGS

A. HELIANTHUS ANNUUS L.

The seeds of *Helianthus annuus* L. germinate rapidly and produce quite sizeable seedlings. The cotyledons are carried above ground by the elongating hypocotyl, and, after the shedding of the seed coats, expand and enlarge to perform the function of foliage leaves. Fig. 47 shows diagrammatically the transition phenomena and characteristic vascular arrangements of the organs of a seedling four or five days old.

The root is tetrarch with four xylem points and four phloem groups forming a square stele with phloem at the corners (Fig. 19). Large cells in the center are not lignified and appear like pith cells in cross section. In longitudinal section these cells in the center of the root are longer than the parenchyma cells of the cortex. A definite pericycle layer is found, from divisions in which lateral roots arise in four rows opposite the protoxylem points. External to the pericycle is an endodermis which is double outside the four phloem groups. This double endodermis is characterized by intercellular ducts. Chauveaud (4) mentions "l'existence d'arcs endodermiques dédoublés avec canaux sécréteurs en dehors des faisceaux criblés" (p. 415). In longitudinal section these ducts are most evident with their heavy contents. The endodermis in longitudinal section has shorter cells than the cortex and is similar to the pericycle. Both cross and longitudinal sections show that the endodermis of the primary root is

pushed out as an outer covering by the secondary lateral roots.
This extension of the endodermis as a covering of the lateral
root is figured by F. O. Bower (3, p. 88) and also by Julius
Sachs (22, p. 150). In Fig. 47, a, the four phloem groups are
lettered A, B, C, D, and the xylem points are numbered 1, 2,
3, 4, for the sake of convenience in description.

In what may be called the "transition" zone where the base
of the hypocotyl and the base of the root connect with struc-
ture atypical of each, the arrangement of vascular tissues is
as in Fig. 47, b. Phloem groups C and D have the same posi-
tion as in the root with xylem groups 3 between them. The
first-formed protoxylem of this group is now isolated between
two lateral later-formed protoxylem groups. Xylem group 1
has a development similar to that of 3. Phloem groups A
and B seem to have split and produced two new groups, A'
and B'. Concerning the behavior of these phloem groups
Chauveaud says, (4, p. 415) "Deaux des faisceaux criblés qui
avoisinent l'un des faisceaux vasculaires correspondant aux
nervures médianes des cotylédons sont continués chacun par
deux fascicules criblés, dont l'un accompagne ce faisceaux
vasculaire, tandis que l'autre se montre écarté de plus en plus
et se trouve situé en dehors du faisceau vasculaire qui cor-
respond à la nervure latérale des cotylédons." Xylem groups
2 and 4 show a lateral development of protoxylem toward
these new phloem groups A' and B'.

At the base of the hypocotyl and to the top of it the struc-
ture shown in Fig. 47,c is found. A' and X(4), B' and X(2)
form collateral bundles at the ends of a slightly elongated
hexagon. Two opposite sides of this hexagonal stele are
occupied by what have been called "double bundles," a term
first used by Miss Ethel Thomas (29). One "double bundle"
consists of two phloem groups with a xylem group between
them, as A, X (1), B of Fig. 47,c. This structure occurs at
some level in the cotyledonary strand of the hypocotyl or
midrib of the cotyledon of most seedlings. The double endo-
dermal arcs continue to be prominent in the hypocotyl. The
pericycle continues also, but is not so characteristic as in the
root.

At the top of the hypocotyl the two collateral bundles which are in the intercotyledonary plane bend sharply outward, splitting into two bundles, each of which forks again, supplying two lateral strands to each edge of the cotyledon. Chauveaud says that these intercotyledonary strands are each represented throughout the hypocotyl "par un vaisseau superposé formant avec la portion criblée la plus récente un groupe cribro-vasculaire qui, au-dessus, se réfléchit et se continue par deux fascicules qui vont aux nervures latérales des cotylédons." (4, p. 416). The "double bundles," after bending outward slightly, continue as the midribs of the two cotyledons. The phloem groups are closer together in the cotyledons and about half-way up the cotyledon the two phloem groups close together to form with the xylem groups a collateral bundle in the midrib. The cotyledons develop four to five rows of palisade tissue on the upper side. Seven or eight rows of cells remain as rather compact parenchyma on the lower side. Stomata develop in the epidermis on both lower and upper surfaces (Figs. 31 and 32).

The transition found in *Helianthus annuus* is described by Chauveaud as quoted above. He did not seem to be interested in the fact that the asymmetrical origin of the intercotyledonary phloem groups is peculiar to this plant. In no other species has such a unilateral "splitting" of phloem been described. As a transition "type" it is distinctive from those already described by Van Tieghem and Miss Sargant.

A series of longitudinal sections was studied to determine the distribution of protoxylem and metaxylem in the primary xylem of the seedling. Only protoxylem with spiral and annular thickenings is found in the young hypocotyl which elongates considerably in *Helianthus annuus*. At the top of the hypocotyl even in an eleven day seedling after considerable xylem has been differentiated, only spirally thickened vessels are found. At this level the earlier formed protoxylem is in the form of much-stretched vessels with isolated rings of thickening.

The petioles of the cotyledons elongate considerably. Con-

sequently they show no metaxylem in the seedlings which were studied.

In the root the growth region is confined to the final five millimeters of the root tip so that as soon as the root has attained any length at all the older basal portion ceases to elongate. This is attested by the fact that in four-day seedlings metaxylem in the form of vessels with a rather open reticulate thickening is found toward the center, while the outer protoxylem of the root poles has fine, stretched spiral or isolated annular thickenings.

At the base of the root and hypocotyl, in the transition zone, the larger, later-formed xylem is metaxylem.

The "double bundle" of the hypocotyl shows a series from the loose spiral protoxylem continuous with the root pole to a close spiral in the vessels of the laterally lignified protoxylem groups.

DETAILED ANATOMY

Seedling 1. The youngest seedlings studied were killed two days after they were planted on filter paper. The young root tip had emerged only 1 or 2 mm. from the seed coats. A series of sections from one of these shows a slight differentiation of phloem in the same position as in older seedlings, namely, four groups in the lower root portion and six groups above in the hypocotyl.

For a distance of about 0.57 mm. from the root tip the sections stain very heavily because of the heavy contents of the young growing cells. All cells have very large nuclei. The structure of the axis becomes increasingly differentiated above this point. However, from this point down to 0.11 mm. from the root tip the central cylinder is distinguishable. At this distance (0.11 mm.) from the root tip the cortical cells are slightly larger and with a little less dense contents than the cells in the central axis. The mostly hexagonal cells are arranged in concentric rows. The radius of the central cylinder or stele (plerome) is six or seven rows of small hexagonal cells, the outer row bounded by a row of circumferentially elongated cells in which an occasional periclinal division has

taken place. Outside this row are four or five rows of larger cells of the periblem which are almost isodiametric and whose cell content appears less dense than that of the central cells or than that of the outer four or five rows of periblem cells. On the outside are several loose rows of root cap cells and a loose seed coat layer. Sections farther up show the continuation of periclinal divisions in the bounding row of cells of the central cylinder in the position of the endodermis, the gradual radial elongation of the cells next inside this latter row into a pericycle layer, and the development of a region of smaller plerome cells inside the pericycle in the position of the later vascular tissue, while the inner cells of the axis have enlarged (Fig. 1).

Higher up, the periclinal divisions in the endodermal layer have become confined to four definite regions, the alternating areas of single endodermis being diametrically opposite each other on the boundary of the central cylinder. Four areas of small cells (protophloem), subtend the parts bounded by double endodermis. In the four equally spaced locations outside the protophloem the pericycle cells are shorter and dividing, adding to the protophloem (Fig. 2). The axial region thus assumes a cruciform symmetry. Intercellular spaces at the corners of the cells in the double endodermal arcs become noticeable. From these ducts develop. The cortex increases in thickness, probably by the division of both the outer and the inner rows of cells. The cells of the central cylinder also increase in number, especially the protophloem and adjoining areas of small plerome cells. A diagram of the situation about 0.50 mm. from the root tip is shown in Fig. 3.

From 0.57 mm. from the root tip to 1.00 mm. there is a gradual change in the arrangement of tissues from the above-described arrangement with the four protophloem groups of root structure to a characteristic hypocotyl structure with six protophloem groups, each subtending its own region of double endodermis. At 0.57 mm. from the root tip it becomes evident that the two adjacent protophloem groups A and B (of one-half of the central cylinder) are larger than the other two,

C and D, and also that the double endodermis above the former two is longer in each case than above the latter. In the two longer zones we find in A nine pairs and in B eleven pairs of endodermal cells as compared with five in C and six in D (Figs. 4 and 5). At 0.67 mm. the eleven pairs of endodermal cells at B are divided into two groups of seven and four pairs respectively, separated by a single cell which has not divided periclinally. The seven pairs (B) mark the position of the original group B of double endodermis while the four pairs (B') are now isolated toward C (Fig. 6). The protophloem group is beginning to be double with more elongated pericycle cells separating the two parts. At 0.72 mm. two undivided endodermal cells separate the double endodermis B from B'. At 0.75 mm. double endodermis A which has increased to twelve pairs of cells is now divided into two parts by two undivided cells, a group of six pairs marking the original position A and four pairs (A') being isolated toward D. There are ten to twelve cells in each of the single endodermis areas except in those separating the newly formed areas A' and B' from their respective progenitors A and B. At succeeding levels higher in the axis these newly formed groups become more evenly spaced until at 1.00 mm. from the root tip the typical hypocotyl structure is but slightly asymmetrical. There is now a central axis whose cross section is in the shape of an elongated hexagon bounded by an endodermis in which occur six almost equally distant double endodermal arcs, next a definite pericycle, then a region of small cells with six areas of small protophloem cells abutting into the pericycle, one subtending each endodermal arc. The central pith cells of the axis are quite large and extend out to the pericycle between the following pairs of phloem groups corresponding to endodermal arcs: A and A', B and B', B' and C, D and A'. A' and B' form the ends of the longest axis of the hexagon (Fig. 7).

This same hypocotyl structure, increasingly symmetrical and spread farther apart by the enlarged pith, is found for a distance of about 2.8 mm. to the base of the cotyledons. As

the distance increases from the root tip, the cells of the stele are more mature. Only the pericycle retains the large nuclei of actively dividing cells. The stele seems to be divided into four definite groups or units composed as follows:

In the cotyledonary plane (the plane joining the midribs of the cotyledons) two long groups each made up of two protophloem groups and their corresponding double endodermal arcs, the now rather indefinite pericycle included, and a narrow region of small cells of pre-xylem between the protophloem groups.

In the intercotyledonary plane two opposite groups composed each of a double endodermal arc, pericycle, a small protophloem area, and a group of small pre-xylem cells bordering the large central pith cells (Cp. Fig. 7).

The first differentiated protoxylem groups appear in the groups in the cotyledonary plane, a single small protoxylem vessel occurring isolated midway between the two phloem groups in the connecting band of small pre-xylem cells. This vessel is midway between the central pith and the outer traces of pericycle. As this first vessel in either of the cotyledonary groups is on a different radius of the cylinder than the phloem, it may be called "xylem alterne" after the method of Chauveaud (4), or alternate xylem. The first vessel begins to appear constantly in each cotyledonary group 3 mm. from the root tip or 2 mm. from the base of the hypocotyl. We now have the beginning of the xylem elements in these two elongated cotyledonary bundles. At this early age no xylem vessels have appeared in the intercotyledonary bundles, whose position, however, is very definitely established by a phloem group, an additional group of pre-xylem cells, and a double endodermal arc (Fig. 7).

At the top of the hypocotyl (3.8 mm. from the root tip) the intercotyledonary bundles appear successively farther and farther removed from each other. The whole hypocotyl is now thicker in this plane as the base of the cotyledons is approached. A cleft starts in from one side before the intercotyledonary bundle has left the stele. These intercotyledonary

strands leave the stele suddenly, bending out almost at right angles, splitting and branching immediately into the two lateral bundles of each cotyledon. The splitting of the cotyledons is asymmetrical, starting on one side and progressing to the other, the bundle supplying the lateral strands to the former side departing first and that supplying the latter departing immediately after. After the departure of the intercotyledonary strands the cotyledonary bundles become gradually farther apart. Two protoxylem vessels are occasionally seen at this level in each cotyledonary bundle, the vessels still being alternate xylem although the two phloem groups of each bundle are slightly closer together. When the cleft separating the cotyledons reaches the central region all the hypocotyl bundles are in the cotyledons and there is left now only a ring of meristematic cells with large nuclei and heavier contents surrounding the pith. By the time the cotyledons are both cut away, the central area is entirely meristematic with a cleft cutting across it in the cotyledonary plane, separating the first opposite pair of stem leaves from a still smaller round apical region which does not extend beyond the base of these leaves. The plumular leaves are 0.68 mm. long.

The cotyledons are thick and composed of twelve to fifteen rows of mostly isodiametric cells bounded by an epidermis of smaller cells on the outside. Acting as a midrib to each cotyledon is the cotyledonary bundle which has continued from the hypocotyl, being now composed of two separated protophloem groups with an isolated protoxylem vessel between them toward the inner surface. This is the so-called "double bundle" which will be mentioned later at greater length. The cells of the cotyledon contain a great deal of oil and protein as stored food.

Seedling 3. This seedling was three days old with root and hypocotyl 8 mm. long, with structure slightly more advanced than that of Seedling 1.

In the root tip the structure is similar to that described in Seedling 1. At 1.00 mm. from the root tip the four double

endodermal arcs are to be seen with the corresponding narrow pericycle and protophloem groups inside them.

The transition to hypocotyl structure takes place in the same manner from 3.0 to 3.5 mm. from the root tip, at which latter distance the six double endodermal arcs and six protophloem groups are definitely established. No protoxylem has as yet been found in the root; a single alternate xylem vessel appears in each cotyledonary bundle 3.6 mm. from the root tip or just at the base of the hypocotyl.

At the top of the hypocotyl in each cotyledonary bundle there is an additional xylem vessel formed at some distance from the first, intermediate in position between the first vessel and one phloem group. This vessel is what Chauveaud calls "xylem intermédiare" or intermediate xylem (Fig. 8). Toward the other phloem group a cell which will form the next cell of intermediate xylem can be recognized. A second or even a third vessel of alternate xylem may be differentiated as is the case in the base of the midrib of one cotyledon (Fig. 9). The phloem is still undifferentiated beyond protophloem. The intercotyledonary bundles even at the top of the hypocotyl show no xylem differentiation beyond the region of xylem meristem internal to the phloem.

In the bases of the first two plumular leaves the central area in each leaf is composed of smaller cells with darker contents, indicating the position of the midrib of the older leaf.

The cells of the cotyledon contain considerable food, especially in the outer layers of the under side where the cells are somewhat smaller than those of the inner or upper surface.

Seedling 4. This seedling (three days old) measured 12 mm. as the total length of the root and hypocotyl. It shows more advance in development than Seedling 3.

The root, which is 4.5 mm. long, shows in its upper part alternate, exarch protoxylem in four places just inside the pericycle. Both cotyledonary and intercotyledonary strands each possess three or four lignified xylem cells, all alternate.

The transition in this more developed seedling shows the

expansion and division of each of the two phloem groups adjacent to one cotyledonary strand. At this same level the xylem in each cotyledonary strand is composed of one or two alternate vessels and to either side of these, two or three cells away, a cell of intermediate xylem. The intercotyledonary strands each comprise a single vessel.

In the base of the hypocotyl, after the phloem groups which split off have assumed their characteristic hypocotyl position at the ends of a slightly elongated hexagon, the xylem of the intercotyledonary root poles and, hence, now of the intercotyledonary strands, is not lignified. It does not reappear until 1.7 mm. above the transition, where a single xylem vessel is seen in one strand. Higher up a vessel appears in the other intercotyledonary strand. This condition persists to the top of the hypocotyl. Throughout the hypocotyl double endodermal arcs cap the six phloem groups. Noticeable intercellular ducts are visible in these arcs. At the top of the hypocotyl the two phloem groups of each cotyledonary strand are relatively closer together than at the base of the hypocotyl.

The intercotyledonary strands leave the top of the hypocotyl to enter the cotyledons as in Seedling 3. In the present seedling, however, lignified elements with annular rings can be distinguished in these lateral traces. The cotyledonary strands are as in Seedling 3 at the base of the cotyledons.

About 1.8 mm. from the base of the cotyledons the midrib bundle shows still a vessel of alternate xylem and four or five vessels of intermediate xylem with the two phloem groups separated only by a band of tissue two or three cells wide. Palisade cells are on the upper inner surface while the cells in the outer part are rounded and parenchymatous.

Seedling 5. This seedling was also three days old with root and hypocotyl 13 mm. long.

The root tip shows the same development as Seedling 1 to the stage with four endodermal arcs 1 mm. from the root tip. 3.5 mm. from the root tip three or four vessels of alternate xylem are lignified at the four poles of the tetrarch root. Farther up the root the amount of xylem in each group is

increased centripetally by more alternate xylem. The four double endodermal arcs remain distinguishable, but are not so striking as in the hypocotyl.

4.5 mm. from the root tip the two phloem groups of one-half of the stele are considerably wider than the other two. There are three vessels of alternate xylem in the cotyledonary xylem group between these two phloem groups and four in the opposite cotyledonary xylem group. The other two xylem groups (intercotyledonary) now each show about three cells of alternate xylem with a cell or two of intermediate xylem developed toward the enlarging phloem groups (Fig. 10). Higher up, the number of alternate xylem vessels in the inter-cotyledonary strands decreases (Fig. 11). At 5 mm. from the root tip the first lignified vessel is separated from the pericycle by an unlignified cell (Fig. 11); the later formed protoxylem cells are either intermediate or superposed ("su-perposé" according to Chauveaud), i. e., on the same radius as the phloem. This xylem is superposed with reference to the new phloem group which has developed laterally and split off from the original root phloem strand (Figs. 12, 13). At 5.4 mm. no alternate xylem has developed, all the xylem being superposed in one strand and both intermediate and super-posed in the other (Fig. 13). The cotyledonary strands at this level contain both alternate and intermediate xylem.

At 5.7 mm. from the root tip the transition to hypocotyl structure is complete, the hexagonal cross section of the stele having been attained. Here at the base of the hypocotyl each cotyledonary strand is composed of one alternate vessel, two intermediate vessels three or four cells away laterally in both directions, and two phloem groups, while each intercotyle-donary strand is composed of two or three superposed vessels and a phloem group. Throughout the transition region peri-cyclic divisions in six areas alternating with the phloem groups show the beginning of the formation of lateral roots. When the transition is complete, i. e., when the intercotyle-donary strands are each a collateral bundle (Fig. 14), the epidermal cells are none of them modified into root hairs.

At the top of the hypocotyl the four bundles are more widely separated, with meristematic indications of plumular strands between the hypocotyl bundles. Each cotyledonary bundle now contains two alternate, and two or three intermediate vessels to either side; each intercotyledonary bundle contains three superposed vessels.

In the bases of the cotyledons (0.7 mm. from where they split), the midrib bundle is further developed by the lignification of a vessel of superposed xylem next to one of the phloem groups (Fig. 15). Higher up more superposed xylem is developed by this time while the two phloem groups are closer together. 2.4 mm. from the base of the cotyledon the two phloem groups of each midrib are no longer separate, but with the xylem form a collateral bundle (Fig. 16).

Seedling 13.   This seedling was grown in soil for five days and had attained a total length of 115 mm. At the enlarged transition region at the bases of root and hypocotyl and for some distance down the root, lateral roots had developed.

The root is about 68 mm. long. Lateral roots are developed in four rows opposite the four protoxylem points. The root is typically tetrarch with four groups of alternate xylem alternating with four phloem groups (Figs. 17 and 18). In the older part of the root toward the base larger vessels of alternate xylem are lignified centripetally (Figs. 19 and 20), followed by several vessels of intermediate xylem (Figs. 21 and 22). As the transition zone is approached the superposed xylem has already lignified opposite the phloem groups and two phloem groups are starting to split (Figs. 23 and 24).

The development of the intercotyledonary strand in a seedling of this age has become complicated by the formation of lateral roots at the transition zone. In the root the two intercotyledonary xylem groups are just like the two cotyledonary ones, each group being composed of alternate xylem. In the transition zone, however, these intercotyledonary xylem groups are laterally increased by intermediate and superposed xylem only on the side toward the two root phloem groups which supply four of the hypocotyl phloem groups (A and B in Figs.

21 and 23). By the greater development of this latter half of the stele the xylem continuous with the two intercotyledonary root poles becomes more lateral in position. The original position of these two protoxylem points is preserved for some distance by the production of lateral roots at these points while the vascular strands are attaining hypocotyl arrangement. Meantime, the development of xylem toward phloem groups A and B and the lateral development of A' and B' result in the formation of two collateral intercotyledonary bundles (Fig. 27). Xylem lignification continues toward the pericycle between phloems A and A' and between B and B', in which locations lateral roots develop. Farther up in the true hypocotyl lateral roots no longer are formed and the xylem connected with them, both the original root protoxylem and the newer lateral extension of later protoxylem of the intercotyledonary strands, is not developed (Fig. 28).

The cotyledonary strands, however, do not change markedly in the transition zone. Each retains its alternate xylem in direct continuation of the root pole, with its bilateral development of intermediate and superposed xylem and its two phloem groups (Fig. 29). The lateral roots arise in the transition zone as in the root, opposite the alternate xylem of the cotyledonary strands.

Typical structure with varying amounts of phloem and xylem persists throughout the hypocotyl. Xylem is most abundant at the base and phloem at the top of the hypocotyl (Cp. Figs. 25 and 27).

In the cotyledons considerable superposed xylem has developed opposite the phloem groups of the midrib bundles, the phloems being closer together (Fig. 26). Alternate xylem and intermediate xylem are evident at the base of the cotyledon, but toward the middle of the cotyledon the midrib becomes a single bundle with one phloem group and all superposed xylem. This bundle continues as the midrib to the tip of the cotyledon (Fig. 30).

Embryos. The cell arrangement of the embryo within the seed is like that observed in Seedling 1, except that root and

hypocotyl together measure only 2.3 mm. instead of 3.8 mm. and that there is no lignification.   Longitudinal sections show elongated strands in the position of future bundles even into the tips of the cotyledons.

E. Fleischer (12) in his embryological studies gives an excellent description of structure in the mature and nearly mature embryo of *Helianthus annuus* that agrees with present observation on Seedling 1 and the embryos in the following points:

1.)   The pericycle is early differentiated at the root tip (12, p. 432).   See also Fig. 1.

2.)   The plerome cylinder is early differentiated into an inner region of large pith-like cells and an outer layer of small cells down into the root tip.

3.)   The central area of pith cells is enlarged in the upper hypocotyl and restricted in the lower root region so that there is a narrow strand of pith in the root which expands in the shape of an inverted cone in the hypocotyl.

4.)   The pericycle is not exclusive to the root but continues as a distinct layer into the hypocotyl, becoming less definite only in the upper part (12, p. 433).

5.)   In the procambium or plerome certain strands develop more strongly than the intervening parts.   Of these there are four in the root and six in the hypocotyl.   Although Fleischer seems to interpret these as destined to become xylem, comparison with all the seedlings of *Helianthus annuus* described in this paper will show that these procambial strands mark the later phloem groups, four in the root and six in the hypocotyl (12, pp. 434-435).

6.)   Next, Fleischer says that four of these six hypocotyl procambial strands enter the cotyledons, each pair pursuing a course parallel to the midrib of each cotyledon.   The two remaining hypocotyl strands in the intercotyledonary plane split and bend sharply outward to supply the lateral veins of each cotyledon.   This is again evidence that the procambial strands are pre-phloem groups, especially those which supply the cotyledon midribs.

SUMMARY OF VASCULAR DEVELOPMENT

Consequently, from the study of embryos one may conclude that the position of the primary tissue of the seedling of *Helianthus annuus* is determined in the development of the embryo within the maturing seed. In the young seedling these tissues progress from an embryonic condition toward a mature one. The enlargement of plerome cells and the thickening of their walls to form xylem vessels and tracheids is a phenomenon accompanying growth. The basic difference in phloem distribution is early determined in embryonic development while the completion of vascular connection in the plant is made as soon as the embryo has to become independent. The vacular transition from root to stem, or really from root to hypocotyl to cotyledons is thus seen to have two phases: the phloem connections already visible in the embryo in the seed, of importance in distributing food to the young, growing seedling, and the later-developed xylem connections which are easily traceable through their various stages of differentiation.

From the above descriptions of seedlings of various ages, it will be seen that a characteristic development of xylem takes place.

In the root four groups of alternate xylem develop within three days from the planting of the seed. These groups of alternate xylem increase by the lateral formation of intermediate and finally of superposed xylem opposite the phloem groups.

In the hypocotyl alternate xylem is developed in the cotyledonary plane two days after planting. Lignification in the hypocotyl starts near the top and progresses downward as the root elongates, so that by the third day lignification reaches the root. In the cotyledonary bundles alternate xylem is soon followed (third day) by intermediate xylem and by the fifth day by superposed xylem.

The intercotyledonary strand of the hypocotyl develops superposed xylem as the first vessel at the top of the hypocotyl, and only at the base of the hypocotyl do alternate or intermediate xylem develop. Here they are an upward continua-

tion of root lignification making a junction with the downward extension of superposed xylem.

At the base of the cotyledons at two days alternate xylem is developed in the midrib "double bundle", but there is no lignification of the lateral strands. At three days the midrib strands have developed intermediate and even superposed xylem in some cases. By the fifth day superposed xylem is abundantly developed in both halves of the "double" midrib and in the lateral strands.

Except in the intercotyledonary strand of the hypocotyl the same developmental series of alternate, intermediate, and superposed xylem may be traced in the seedling of *Helianthus annuus*. These are the three phases of Chauveaud's second cycle of individual and evolutionary development. This is the basis for his theory of basifugal acceleration, namely, that the rapidity of development increases as the distance from the base of the hypocotyl with a consequent shortening, disappearance, or even failure of development of the earlier phases of the cycle. In the cotyledonary strands of *Helianthus annuus* the first case of acceleration is illustrated by the earlier appearance of alternate xylem at the top of the hypocotyl and in the cotyledons, of intermediate xylem in the cotyledons and the top of the hypocotyl before the base, and of superposed xylem in the cotyledons before the hypocotyl. The intercotyledonary strand is composed entirely of superposed xylem, according to Chauveaud's theory, because of the telescoping of the alternate and intermediate stages as in the upper part of the cotyledon midrib. The shortening of the early phases is shown by comparison of the one or two alternate vessels of hypocotyl and cotyledons with the large development of alternate xylem in the root. The hypocotyl develops more intermediate xylem than the cotyledon bases. The proportion of superposed xylem developed increases toward the top of the hypocotyl and cotyledons.

Chauveaud traced differentiation of alternate, intermediate, and superposed phloem in some of his plants. Here this has not been attempted. The position of the primary phloem is

fixed in embryonic development, and its actual differentiation is not so striking as that of the xylem. Food-conducting paths are probably more important in starting root and hypocotyl growth than water-conducting tissue. Vessels are increasingly important as the above-ground parts increase in size and the underground parts must meet the increasing demands for water. Consequently, their position becomes evident only after growth starts.

B. ARCTIUM MINUS BERNH.

The seeds of *Arctium minus* Bernh. are slow to germinate; the root tip pushes out of the seed-coat about six days after the seeds are planted. The seedlings are less massive than those of *Helianthus annuus* and subterranean except for the two cotyledons which appear above ground about eleven days after planting. They expand and serve as foliage leaves.

A diagrammatic representation of the arrangement of tissue in a seedling thirteen days after planting is shown in Fig. 48.

The root and base of hypocotyl show diarch root structure as in a and b of Fig. 48. In the seedling there is a slight but sudden increase in diameter of the axis somewhat below the cotyledonary node. Just below this bulge the first lateral roots arise, opposite the two xylem points of the stele. There is additional internal evidence which may be considered in delimiting the root and hypocotyl. Just above the first and uppermost lateral root the sections shown an increased diameter without any difference in the diameter of the stele. The epidermis above this level has no root hairs, and there are no lateral roots. In the stele itself certain differences may be noted. In the root there are only one or two small vessels marking each protoxylem point of the diarch stele. Lignification proceeds centripetally, producing successively larger vessels until later a diarch plate is probably formed as noted by Lee (21) in *Arctium majus* Bernh. In the root of the seedlings which were studied, the central cells of the stele are large and destined to become xylem vessels. In the part of the axis

which is designated as hypocotyl the central cells of the stele are small, there are many (6 - 8) small protoxylem cells inside the pericycle, and later lignification tends to proceed laterally rather than centripetally. The two phloem groups of the stele are more elongated in the hypocotyl than in the root. An additional feature of the hypocotyl is that in the upper part two additional xylem groups (1a and 2a, Fig. 48) start and proceed downward to eventually connect laterally with groups $X(1)$ and $X(2)$ respectively.

The stele of the root and hypocotyl are alike in that both are surrounded by a pericycle layer. The inner cortical cells are arranged radially in rows with intercellular spaces; the inner row next to the pericycle shows no specialization in the young seedlings studied. In *Silybum Marianum* Chauveaud figures "un cercle sécréteur" which resembles the condition in the inner cortex in *Arctium minus* (4, p. 403). Fig. 40 shows some of this "secretory" layer. Lateral roots arise in the pericycle of the primary root and the inner layer of the cortex (endodermis) is carried out by the growing root as in *Helianthus annuus*.

At the top of the hypocotyl each phloem group becomes separated into three distinct groups (Fig. 48,c), and the stele of the hypocotyl becomes separated into four bundles which enter the cotyledon petioles. These are united in a tube for almost 2 mm. The "double bundles" in the cotyledonary plane which become the midribs of the cotyledons are composed as follows: phloem A' and B' and between them xylem group 1 continuous with the original root pole; phloem A''' and B''' and between them xylem group 2 continuous with the root pole. Alternating with these "double bundles" are the two collateral bundles of the intercotyledonary plane which pass into the cotyledonary tube and split to supply a lateral bundle to each cotyledon. Each collateral bundle is composed of a phloem group A'' or B'' continuous with the root phloem and a later lignified xylem group 1a or 2a whose connection with root xylem is indirect.

When the cotyledonary tube splits through completely, the

base of each cotyledon contains three bundles, two small laterals and a larger midrib bundle which becomes collateral higher up since the two phloem groups develop closer and closer together at higher levels until the "double" structure is gone (Fig. 48, d and e).

This transition agrees with Lee's brief note on *Arctium majus* (21, p. 320) : "The xylem of the lateral strands remains distinct in the center of the hypocotyl for a long distance before finally merging into the xylem of the midrib bundles to form the diarch plate."

DETAILED ANATOMY

Seedlings 2a, 2b, 4a. These seedlings were nine days old. 2a and 2b were grown on filter paper and measured 22 and 20 mm. in length, respectively. 4a, grown in soil, was 27 mm. long and the cotyledons were still contained within the seed-coats underground. The difference in length of the three seedlings is mainly in the roots as in all of them the cotyledons are about 5 mm. long, the cotyledonary tube 0.5 mm., and the hypocotyl 2 to 2.2 mm. long. The vascular development is at the same stage in all, and no lateral roots had yet appeared.

For about 3 mm. back from the root tip there is no lignification. About 5 mm. from the root tip the two root poles have each been established by the lignification of two vessels of alternate xylem. Small areas of differentiating phloem alternate with these xylem groups. Higher up in the root in the older basal portion two larger vessels of alternate xylem have developed and the phloem areas are also larger (Fig. 33). The central cells of the stele are large and destined to become vessels. The stele is bounded by pericycle and endodermis.

At the base of the hypocotyl the stelar arrangement is root-like in that all the xylem is alternate. Pericycle and endodermis are continuous with these tissues of the root. However, root hairs are not developed; the central cells of the stele are smaller and undifferentiated. Here at the base of the hypocotyl the three or four alternate xylem vessels are arranged with two or three touching the pericycle and only

one internal to these. About the middle of the hypocotyl each xylem group consists of three alternate vessels in a row parallel to the pericycle and separated from it by a row of unlignified cells (Fig. 34). The stele increases slowly in diameter toward the top of the hypocotyl, and the central tissue is pithlike.

At the top of the hypocotyl each phloem group has become three. Each cotyledonary xylem strand is composed of two or three vessels of alternate xylem (Fig. 35). Slightly higher up each xylem group, accompanied by the two phloem groups bordering it, is removed from the central stele and the remaining two phloem groups are each in a lateral position, leaving only a cylinder, or really a cone, of meristematic tissue in the center of the axis. Each xylem group with its two phloem groups becomes the "double bundle" destined to be the cotyledon midrib. The "double bundle" structure is present in 9-day seedlings in the cotyledonary tube and into the base of the cotyledon. Here it is composed of the two phloem groups and two or three vessels of alternate xylem and also one or two of intermediate xylem (Fig. 36). About 0.75 mm. above the top of the tube superposed xylem is present in the midrib and the two phloem groups are closing together. 1 mm. from the top of the tube the midrib is a collateral bundle with one phloem group and all superposed xylem (Fig. 37).

The central one of the three phloem groups found on either side of the xylem at the top of the hypocotyl in the inter-cotyledonary plane, passes into the cotyledonary tube, where it almost immediately splits to supply a lateral strand to each cotyledon. In the 9-day seedling each of these lateral strands of the cotyledon is composed of a phloem group and one or two vessels of superposed xylem (Fig. 38). The single phloem group, when it first enters the cotyledonary tube, is accompanied by one or two vessels of superposed xylem. At a lower level in the top of the hypocotyl there is no xylem representing the lateral intercotyledonary strand except a single superposed vessel in Seedling 2b.

The cotyledons and hypocotyl are packed with stored food.

Plumular development is slight at this stage. The first plumular leaf is only 0.2 to 0.3 mm. long and the second leaf is not separated from the stem tip.

Seedling 6. This seedling was killed 13 days after the seeds were planted in soil. The total length of root and hypocotyl was 68 mm., the whole seedling measuring 76 mm. The petiolar tube of the cotyledons is 1.8 mm. long, and the hypocotyl is 6 mm.

Near the base of the root, 6 mm. below the base of the hypocotyl, the stele shows the additional lignification of alternate xylem since the 9-day stage (Compare Fig. 39 with Fig. 33).

The base of the hypocotyl is definitely distinguishable 6 mm. below the beginning of the cotyledonary tube. The central cells of the stele are small. Half way up the hypocotyl the two phloem groups have developed laterally until three groups of differentiated phloem are discernible (Fig. 40). At this same level one vessel of superposed xylem is lignified in the intercotyledonary plane opposite the middle phloem group on one side of and toward the center of the stele. 2 mm. below the beginning of the cotyledonary tube each group of xylem in the cotyledonary plane is composed of four or five alternate and two laterally formed intermediate vessels, while the intercotyledonary xylem groups are each composed of three superposed vessels (Fig. 41).

At the top of the hypocotyl the cotyledonary strand of xylem is composed mainly of intermediate vessels with a few alternate ones. Larger parenchyma cells now separate the three phloem groups of each half of the stele so that the four bundles are recognizable before they leave the stele: two cotyledonary strands, "double bundles" (Fig. 42), and two intercotyledonary strands, collateral bundles (Fig. 43).

In the lower part of the cotyledonary tube the lateral intercotyledonary strands split to supply each cotyledon petiole with two lateral strands with three or four superposed vessels each. At the top of the tube each petiole contains three bundles. The midrib is still "double" (Fig. 44). Intermediate

xylem is considerably developed, but the two alternate vessels present in the 9-day seedling (Fig. 36) are in the process of resorption.   This resorption is an evidence of basifugal acceleration (See p. 436).

2 mm. above the top of the tube, the midrib is no longer "double," but a single collateral bundle with superposed vessels only and but one phloem group (Fig. 45).   At the same level each lateral bundle has 3 - 8 vessels of superposed xylem (Fig. 46).

In this 13 day seedling the first plumular leaf is 0.9 mm. long and the second one is definitely separated from the meristematic stem tip.

Embryos.   Mature embryos from the seeds were secured as in *Helianthus annuus.*   The total length averaged about 4 to 4.5 mm., with radicle and hypocotyl measuring 1.25 mm.

Cross sections of the embryo of *Arctium minus* show near the root tip a decided separation of the small cells of the stele or central cylinder from the surrounding large cells of the cortex.   All cells are heavily packed with oil and protein food particles which stain deeply with safranin.   About 0.7 mm. from the root tip the cells of the central stele show a decidedly paler staining than the cortical cells, especially in a ring surrounding darker-stained central cells.   1.1 mm. from the root tip this ring begins to spread and it becomes separated at about 1.2 mm. into four groups of pro-vascular tissue which pass out of the stele in four directions.

Two groups leave the central cylinder in the cotyledonary plane to form the midribs of the cotyledons.   Each midrib strand upon close examination is seen to be composed of two small groups of pre-phloem cells separated by a small area of pre-xylem.   These pre-phloem areas are closer together higher up in the midrib until they form a single group.   Higher in the cotyledon the whole strand is a single meristematic group. This midrib structure in the embryo is easily correlated with that of the older, growing seedling, the whole strand being the undeveloped "double bundle."

The other two pro-vascular groups pass out laterally in

the intercotyledonary plane and split each into two groups before the cotyledons split apart. As in the seedling each lateral strand contains but a single pre-phloem group.

Here as in Seedling 1 of *Helianthus annuus* there is no cotyledonary tube, the cotyledons splitting as in the former plant from one side to the other.

So, it appears that in *Arctium minus* as well as in *Helianthus annuus* the phloem distribution is determined in embryonic development within the seed and the vascular transition from root through hypocotyl to cotyledons again resolves itself into the two phases: the embryonic phloem connections and the later-maturing xylem connections.

SUMMARY OF VASCULAR DEVELOPMENT

Briefly reviewing the development of vascular tissue in *Arctium minus*, we find first that the phloem connections are already established in the mature embryo. Xylem is differentiated when the seedling starts to grow. Alternate xylem develops first in root, hypocotyl, and cotyledon bases. At nine days intermediate xylem is already differentiated in the "double bundle" of the cotyledonary tube, while superposed xylem is present midway in the cotyledon midrib. At thirteen days more alternate xylem has lignified in the root, intermediate xylem has appeared at the top of the hypocotyl, while in the cotyledonary tube the first-formed alternate xylem is disappearing due to resorption, and more intermediate xylem has been differentiated. Superposed xylem has increased higher in the cotyledon.

Thus, in the cotyledonary strand from root to cotyledon a series may be traced showing the successive development of alternate, intermediate, and superposed xylem. The farther from the root the earlier is the appearance of the later stages and the smaller the development of the earlier stages. This is again an instance of basifugal acceleration (p. 436). In *Arctium minus* the acceleration is manifested by the additional feature of the resorption of the alternate xylem of the midrib

bundle. Higher up both alternate and intermediate phases are telescoped and only superposed xylem appears.

The intercotyledonary strand also shows acceleration, only superposed xylem appearing from the beginning. The vessels are first differentiated in the cotyledons and lignification proceeds downward. This is exactly as in *Silybum Marianum* (L.) Gaertn., *Cichorium amara*, *Centaurea Cyanus* L., and *Carthamus tinctorius* L. described by Çhauveaud (4).

III. DISCUSSION

THE HYPOCOTYL

A comparison of hypocotyls in *Helianthus annuus* and *Arctium minus* immediately shows that hypocotyl structure is not constant. Nevertheless, root and hypocotyl are distinct in both plants.

Lamarck in 1786 first mentioned "le collet de la racine" or "top of the root." The early idea was that the collet was a plane separating root and stem. Clos (5) in 1849 was the first to reject the idea of a complete separation of root and stem and advised designating as the collet "toute la partie de l'axe comprise entre les cotylédons et la base de la racine, désignée elle-même par le lieu où commencent à se montrer les rangs réguliers et symétriques des radicelles." In *Helianthus annuus* four rows of lateral roots characterize the root while six develop in the transition zone. These are absent in the hypocotyl. In *Arctium minus* lateral roots are absent in the hypocotyl.

Van Tieghem in 1896 described the "collet" as the place where the rotation of protoxylem from an exarch to an endarch position, and the superposition of xylem against phloem occur. Dodel in 1872 also took division of the root bundles and rotation of protoxylem as criteria. The lack of root hairs as epidermal appendages was also taken as a criterion to distinguish hypocotyl from root. This is seen to apply in the two seedlings here described.

Gérard (14) conservatively states: "le collet est une ré-

gion, plus ou moins étendue, dans laquelle l'axe présente des états transitoires entre les structures types de la racine et la tige. La changement d'épiderme n'est qu'une des phases de ce passage."

Recent studies show that the hypocotyl is intermediate not between root and stem, but between root and cotyledons. Root structure is definite. Vascular arrangements vary in hypocotyl and cotyledons, although the series in the midrib is the same in all cases: a lateral development of intermediate and superposed xylem and a disappearance and failure to develop of alternate and intermediate xylem until all the bundles in the cotyledon are collateral. Broadly applying Gérard's definition the "collet" is the hypocotyl in which the transition stages from root structure to stem structure occur.

Hypocotyl and cotyledons have actually one vascular system to which the later developed vascular system of the plumule connects downward. It might be well to consider the hypocotyl and cotyledons as the seedling "shoot" as distinguished from the root. Hypocotyl is thus a primitive stem in that its vascular system is continuous with that of the primitive leaves, the cotyledons.

THE COTYLEDONS

The cotyledons of *Helianthus annuus* and *Arctium minus* differ from the plumular leaves which develop later in the absence of epidermal hairs, the comparatively simple venation, and in the "double bundle" structure of the midrib.

BASIFUGAL ACCELERATION

Based upon extensive ontogenetic studies of seedlings in many groups of plants, Chauveaud's theory of the evolution of the conducting apparatus of plants through successive phases was developed (4). Each phase is characterized by a special arrangement of vessels and sieve tubes. These phases he grouped in two cycles, of which we are concerned with the second including the alternate, intermediate, and superposed phases. The phases of the two cycles are succes-

sive stages in a general type of conducting system. The alternate root arrangement and superposed stem arrangement are not comparable, and the inverse relation of these two types cannot be explained by splitting and rotation of protoxylem because these do not take place. Root and stem are different because they represent different phases.

The stem has not preserved the ancestral character maintained in the root. In the stem of most plants the vascular evolution has undergone more or less acceleration. The early phases of the second cycle are represented at the base of the hypocotyl though suppressed at the top by basifugal acceleration. Resorption and secondary development later obscure what may have occurred in the first phases. In the root no such acceleration takes place, and, consequently, only the ancestral character of the alternate phase persists.

It appears, therefore, that the young root is constant in arrangement while the young stem has an arrangement varying with its degree of evolution. Therefore, the union of the two is not uniform. If, as is most commonly the case, the hypocotyl has the arrangement corresponding to the alternate phase and the same number of strands as the root there is no transition, properly speaking. There is perfect vascular continuity.

In the second cycle the foliar trace acquires the superposed arrangement, preceded by the intermediate and alternate arrangement as is shown by the cotyledons in the Phanerogams.

The ontogenetic basis for this theory of Chauveaud's is so strong that I have used the alternate, intermediate, and superposed phases of the second cycle as phases in the development of the individual seedling. This ontogenetic development and the principle of basifugal acceleration have already been shown to be exemplified by *Helianthus annuus* (pp. 435-437) and by *Arctium minus* (pp. 440-441).

The shortness of these phases and their rapidity of succession in seedling development favor a recapitulation theory, but seedling development is a physiological process in which

many factors affect the seedling. Compton (7) concludes that the intermediate phase is only of physiological importance. The alternate phase is also of physiological significance in an underground part like a root where nearness to the water supply is advantageous.

EMBRYOS

Embryos of *Helianthus annuus* (p. 435), *Arctium minus* (p. 440), and *Taraxacum officinale* Weber (25), show plerome tissue and, especially, pre-phloem in the position of later phloem strands. Xylem becomes specialized later than phloem when the seedling begins to grow. With Lee (21) we may conclude "that physiological factors are not sufficient to account for all the structures found in seedlings."

THE COTYLEDONARY STRAND

The "double bundle" of the cotyledonary strand is a common feature of seedlings. Various interpretations have been placed on this occurrence of an isolated protoxylem vessel between two groups of almost collateral xylem and phloem. Compton (6) speaks of the "double bundle" as a "triad" of xylem groups, a terminology also used by A. Gravis (15). Gérard (14) mentions the splitting of the xylem group and the isolation of the two branches from the protoxylem vessel. Van Tieghem (31) and Hill (16) use the term "splitting" in describing the behavior of the xylem. Chauveaud (4) greatly opposed this common mode of describing xylem groups as splitting. In his paper we find frequent reiterations that rotation and splitting are only illusions produced by the arrested development of earlier stages and acceleration of later stages of vascular development.

The xylem of the cotyledonary strand is always continuous with a xylem group of the root. In seedlings with diarch roots the phloem groups of the "double bundles" are produced by the lateral development and separation of the two phloem groups of the root (Fig. 48). In the usual tetrarch type the phloem groups of the "double bundles" continue from the root, but each contributes a half to the phloem group of the inter-

cotyledonary bundle. In *Helianthus annuus* the splitting of phloem groups is confined to one-half of the stele only, so that one-half of the root phloem is in direct continuity with the phloem of only one cotyledonary strand (Fig. 47).

In different species the "double bundle" occurs at different levels in the seedling. In some species, e. g., *Arctium minus* and *Taraxacum officinale*, it occurs only at the top of the hypocotyl and into the midribs of the cotyledons. In *Helianthus annuus* it develops at the base of the hypocotyl and continues into the base of the cotyledons. *Piper cornifolium* HBK. and *P. geniculatum* Hort. ex Link., described by Hill (16) have the "double bundle" in the hypocotyl, a single collateral bundle replacing it in the petiole of the cotyledon. According to Chauveaud's theory of basifugal acceleration, the first type is least accelerated, the second more, and *Piper* most accelerated.

If any part of the seedling structure is of phylogenetic significance the cotyledonary strand with its constant type of development is that part. However, the double leaf trace may hardly be looked upon as an incipient dichotomy (29) since many studies show that the "double bundle" closes over in the cotyledon.

THE INTERCOTYLEDONARY STRAND

The intercotyledonary strand presents more of a problem than the cotyledonary strand. Most seedlings with tetrarch roots possess in the hypocotyl an intercotyledonary strand which divides at the top of the hypocotyl to supply lateral veins to the cotyledons. This intercotyledonary strand is always a collateral bundle with a phloem group derived usually by the lateral development of phloem from each of the two adjacent root phloem groups, or in the exceptional case of *Helianthus annuus*, from only one of these adjacent phloem groups (Fig. 47,b).

The occurrence of lateral strands in the hypocotyl of seedlings with tetrarch roots may well raise the question of the relation of the intercotyledonary or lateral strand to the symmetry of the root. In describing a seedling of *Impatiens*

Balsamina L. which has a tetrarch root, Chauveaud says (4, p. 334) that the intercotyledonary bundles undergo great acceleration, in that their alternate vessels are suppressed, that their intermediate vessels are widely separated and followed soon by superposed xylem. In *Helianthus annuus* this may be traced at the base of the hypocotyl (p. 433). Before this development occurs, however, superposed xylem appears toward the top of the hypocotyl (p. 432) and connects downward later.

In *Arctium minus* where the root is diarch, the lateral strand lignifies first at the top of the hypocotyl, and then downward to connect with the inner vessels of the diarch stele, Lee (21) found this type commonest among the fifty Composites he studied. Of *Silybum Marianum* which is also of the type of *Arctium minus* Chauveaud (4) says that due to the early appearance of superposed xylem only in the laterals of the cotyledons these strands present a greater acceleration than the midribs which retain for a short while alternate vessels. The lignification downward of the superposed xylem of the lateral strand is a development parallel to that of the midrib in which superposed xylem appears first at the top and then farther and farther toward the base.

May not diarchy or tetrarchy in a root be independent of the lateral strands of the hypocotyl and cotyledons? The downward lignification of the lateral strands suggests an independent development from that of the root poles. However, the lateral development of the xylem in these root poles in the transition region of *Helianthus annuus* suggests an identity of root lateral and hypocotyl lateral. The absence of lateral root poles in *Arctium minus* shows that at least in this species the hypocotyl laterals do not affect root symmetry.

DIARCHY AND TETRARCHY

Compton (6), after studying the *Leguminosae* where tetrarchy characterizes large seedings of species with large seeds and the tree habit, concludes that the tetrarch root stele is primitive and the diarch derived. Lee (21) does not find

the same correlation of tetrarchy and large seedlings in the herbaceous Composites he studied, and he feels that either diarchy or tetrarchy may have been derived several times in the course of evolution. Chauveaud (4) in advancing the theory of the acceleration of the laterals intimates a later and more advanced development of the laterals. He makes no statement as to which type of root symmetry is primitive.

THE LEVEL OF TRANSITION

Van Tieghem's types of transition are based on a supposition that the hypocotyl possesses stem structure. In his description of the three types (31, p. 782) he does not mention the cotyledons or their vascular arrangement. However, most workers have described the vascular arrangements in root, hypocotyl, and cotyledons of younger seedlings than Van Tieghem used. Transition phenomena are those occurring between root and cotyledons in one continuous vascular system. Inasmuch as the cotyledon midrib attains higher up the collateral arrangement of the bundles of stems there is actually a developmental transition from root structure to stem structure.

Compton (6) defines three levels of transition: "high," where the transitional changes do not occur until high in the hypocotyl, which retains for most of its length a root-like structure; "low," where the transitional phenomena begin below the external limit of the hypocotyl and are complete at the base of the hypocotyl, (i. e., more or less stem-like collateral bundles have been produced and the root protoxylem may or may not persist in the hypocotyl) ; "intermediate," in which the completion of transition is stretched through the hypocotyl. Following a suggestion of Gérard's, Compton correlated the transition level with the volume of the hypocotyl. This volume he computed by the formula $\pi L \left(\frac{R+r}{2}\right)^2$, where L is the average length of hypocotyl, R is the radius at the base of the hypocotyl, and r is the radius at the top. He classified his plants according to transition level, took the average measurements for the more than thirty plants in each group, and computed the average hypocotyl volume for the

three levels of transition as follows:　Low - 229.6 cu. mm., Intermediate - 23.6 cu. mm., High - 8.3 cu. mm.

This test was applied to the seedlings described in this paper:[1]

Seedling	L	2R	2r	Vol.
Helianthus annuus	40 mm.	2.4	2	152.4
Arctium minus	6 mm.	1.1	1.4	7.4

Helianthus annuus has a low transition and a hypocotyl volume of 152.4 comparing favorably with Compton's figure of 229.6.　*Arctium minus* has a high transition and a hypocotyl volume of 7.4 close to Compton's 8.3.

Lee (21) finds in the *Compositae* many exceptions to the rule that size of seedling is correlated with the type of structure.

The different habits of the seedlings of *Arctium minus* and *Helianthus annuus* suggest that the level of transition might be correlated with the habit.　The hypocotyl of *Helianthus* rises stem-like into the air, and its structure is nearer stem structure in the possession of the "double bundle" and the presence of pith than that in the subterranean hypocotyl of *Arctium minus* which retains a stelar structure almost rootlike for much of the hypocotyl length.　Seedlings of *Taraxacum officinale* (smaller than *Arctium minus*) exhibit a high transition and a habit similar to that of *Arctium minus*. After the cotyledons are enlarged and expanded *Taraxacum* produces a small rosette, leaf by leaf.　The two cotyledons of *Arctium minus* expand just above the soil level and the seedling develops into a rosette as the plant is a biennial.　No conclusions may be drawn until more data are available concerning the level at which the soil line strikes the axis of epigeal seedlings.

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[1] In both species measurement showed that the diameter of the hypocotyl is constant except that the base is smaller in very young seedlings, while the length increases with age.　In *Helianthus* the length used above is for 5-day seedlings.　In *Arctium* the length is for a 13-day seedling.

TYPE OF TRANSITION

The type of transition is a diagrammatic representation of the disposition of the vascular strands in the seedling. Lee (21) finds a single basic type of transition in the *Compositae* with extreme and intermediate cases. The seedlings with tetrarch root and laterals throughout the hypocotyl of the type of *Bidens pilosa* are at one end of the series. *Helianthus annuus* (Fig. 47) varies from this type in the derivation of the intercotyledonary phloem groups. If in Fig. 47 small phloem groups C' and D', corresponding to A' and B', split off and fused, A' with D', C' with B', the transition would be as in *Bidens pilosa*.

Arctium minus (Fig. 48) corresponds to the commonest and intermediate type in which the root is diarch and each phloem group supplies three strands in the upper hypocotyl, the laterals not connecting to the root.

Cichorium Intybus is the third type and the other extreme described by Lee. The root is diarch, each phloem group divides only into two and the cotyledons receive only the midrib from the hypocotyl. This type is found also in *Taraxacum officinale*.

ENDODERMIS

The layer of cells external to the pericycle which is double over the phloem groups in *Helianthus annuus* has been interpreted in the present instance as endodermis, as Chauveaud interpreted it. His description of *Helianthus annuus* has already been quoted (p. 428). In *Calendula officinalis* the situation is as in *Helianthus annuus*: "L'endoderme offre des canaux sécréteurs quadrangulaires disposés suivant deux arcs en dehors des faisceaux criblés. Dans l'hypocotyle, en dehors des faisceaux vasculaires, l'endoderme est simple et sans méats," (4, p. 410). *Zinnia elegans* is like *Helianthus annuus*: "En dehors de ces quatre demi-faisceaux criblés il y a un arc sécréteur endodermique bien développé," (4, p. 410.) In *Dahlia coccinea* and *Tagetes lucida* the phloem groups of the primary root and of the hypocotyl are accompanied by double endodermal arcs.

A double endodermis is nowhere else described. DeBary says: "The endodermis is a sheath consisting in all cases of one single layer of cells" (9, p. 121). According to Strasburger (27, p. 90), the innermost layer of cells of the cortex in the mature subaerial stems of land plants may be developed as a starch-sheath or as a typical endodermis, especially in the subterranean shoots of land plants and in the stems of aquatic plants. In roots (27, p. 128), the innermost layer of the cortex is usually developed as an endodermis which sharply marks the limit between cortex and central cylinder.

In free hand sections of the hypocotyl of *Helianthus annuus* stained with iodine the starch sheath or phloeoterma is seen to be a single layer of cells outside the pericycle. Opposite the six phloem groups the starch-containing cells form only a single layer beyond which extends into the cortex a layer or two of cells which are different from the cells of the cortex but without starch grains. These are the endodermal secretory arcs of Chauveaud's descriptions.

In *Silybum Marianum* Chauveaud's drawings show a condition similar to that in *Arctium minus*. Of this "cercle sécréteur" he says, "L'endoderme de la radicule, disposé en files radiales régulières avec les assises corticales internes, conserve cette disposition jusqu'au sommet de l'hypocotyle . . . . à la base des cotylédons on le retrouve seulement en dehors des faisceaux médians où il forme un arc sécréteur limité aux bords du faisceau." (4, p. 408). The situation in *Arctium minus* where the inner cortex is composed of radial rows of cells is probably due to the immaturity of the cortex of the seedlings. W. Ralph Jones (19) describes a similar condition in young seedlings of *Dianthera americana* L. in which the endodermis is not yet specialized. The restriction of these radial rows to a position outside the phloem groups at the base of the cotyledons in *Silybum Marianum* suggests that the restriction of the "double endodermis" in seedlings like *Helianthus annuus* may also possibly be correlated with immaturity of the tissues.

IV.   CONCLUSIONS

1.   The cotyledons of *Helianthus annuus* and *Arctium minus* function as leaves, but differ from the plumular leaves in the absence of epidermal hairs and in the presence of the "double bundle" structure in the midrib.

2.   The hypocotyl-cotyledon vascular system develops first and the plumular traces are established later in the hypocotyl of *Helianthus annuus* and *Arctium minus*.

3.   There is no vascular transition from root to stem, but there is a developmental transition from root arrangement to stem arrangement in the vascular elements of the midrib strand of the cotyledons.

4.   Chauveaud's theoretical phylogenetic sequence of alternate, intermediate, and superposed arrangements of vascular tissue may be traced in the ontogeny of the vascular tissue of the hypocotyl and cotyledons of *Arctium minus* and *Helianthus annuus*.

5.   Embryos show the presence of plerome areas and pre-phloem groups.   Embryological studies are necessary to show the ultimate factors in determining seedling vascular arrangements.

6.   The "double bundle" structure occurs in the cotyledonary strands of *Helianthus annuus* throughout the hypocotyl and into the base of the cotyledons.   In *Arctium minus* it occurs from the top of the hypocotyl into the base of the cotyledons.   In both, basifugal acceleration is exemplified.   If any part of the seedling structure is of phylogenetic significance it is the cotyledonary strand with its constant type of development.

7.   The intercotyledonary strand of the hypocotyl of *Helianthus annuus* shows great acceleration and is only indirectly continuous with the corresponding root pole.

8.   *Helianthus annuus* with a low transition level has a large hypocotyl volume.   *Arctium minus* with a high transition level has a small hypocotyl volume.

9. The transition level can possibly be correlated with seedling habit when more data are available.

10. Three variations of a single type of transition are found in the Compositae. The extreme diarch variation is seen in *Taraxacum officinale* which is not described here. *Helianthus annuus* though tetrarch does not exhibit the typical behavior of phloem. *Arctium minus* is of the commonest type with a diarch root and lateral strands only at the top of the hypocotyl.

11. The double endodermal arcs described by Chauveaud in the radicle and hypocotyl of Composite seedlings are not described elsewhere in the literature. These areas of tissue in *Helianthus annuus* differ from the cortex in the small size of the cells and from the endodermis (or phloeoterma) only in the absence of the starch. In *Arctium minus* the inner cortex in young seedlings is as yet undifferentiated into endodermis and cortex.

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EXPLANATION OF PLATES

In the diagrams phloem is stippled and xylem is hatched. Xylem groups are numbered (1), (2), (3), (4), while phloem groups and, in Figs. 3 and 7, double endodermal arcs are lettered A, B, C, D. The following symbols are used throughout the drawings:

End.	Endodermis
Per.	Pericycle
pl.	plerome
pp.	protophloem
Ph.	primary phloem
xa.	alternate xylem
xi.	intermediate xylem
xs.	superposed xylem
LR.	lateral root

Figures 1-32 are of *Helianthus annuus.*

PLATE I

FIGS. 1-5.   Seedling 1, two days old.

FIG. 1.   Stele .25 mm. from root tip showing differentiation of large central cells, plerome, pericycle, and endodermis; x 300.

FIG. 2.   Detail of about one-fourth of stele .5 mm. from root tip, showing endodermal arc B, pericycle, and pre-phloem group; x 300.

FIG. 3.   Diagram of stele .5 mm. from root tip. The double endodermal arcs are lettered to correspond to the phloem groups which are developing below them. The position of future xylem is indicated by numbers; x 72.

FIG. 4.   Detail of area of stele .57 mm. from root tip showing elongated double endodermal arc B of eleven pairs of cells; x 300.

FIG. 5.   Detail of area of stele at .57 mm. from root tip showing double endodermal arc C of seven pairs of cells; x 300.

1.

pl
Per
End

5.

Per
End
pp

B
C
End
Per
pp
A
D
3.

2.

pp
Per
End

4.

End
p.p
Per
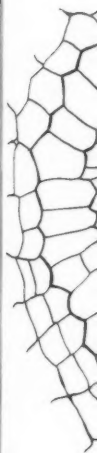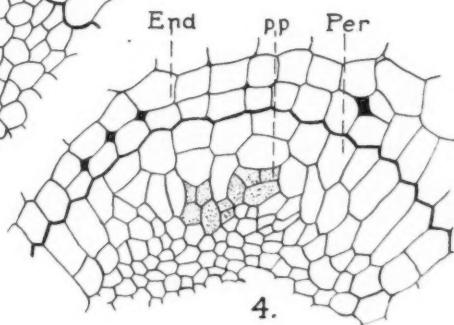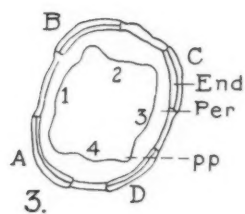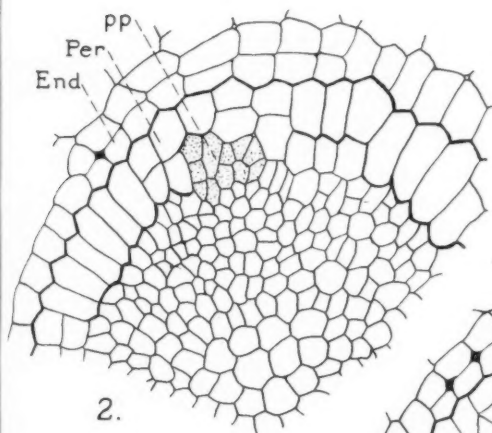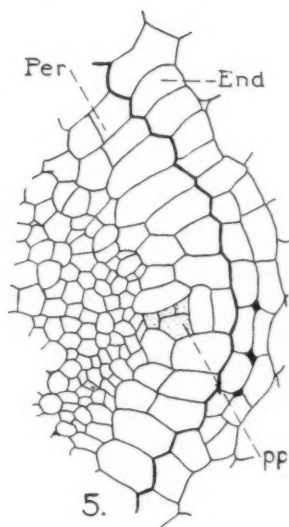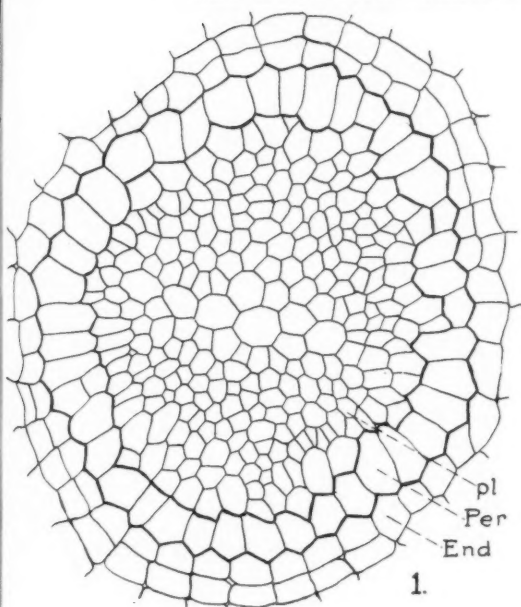
PLATE II

FIGS. 6 AND 7. Seedling 1, two days old.

FIG. 6. Detail of area of stele .67 mm. from root tip, showing double endodermal arc B separated into two groups B and B' by a single cell (e); x 300.

FIG. 7. Diagram of stele .67 mm. from root tip; x 72.

FIGS. 8 AND 9. Seedling 3, three days old.

FIG. 8. Part of cotyledonary strand at top of hypocotyl; x 300.

FIG. 9. Portion of midrib at base of cotyledon, showing three alternate vessels, intermediate vessels forming; x 300.

FIG. 10. Seedling 5, three days old. Detail of intercotyledonary root pole 4.7 mm. from the root tip, showing the beginning of transition to hypocotyl structure. The original root pole is marked by alternate vessels. An intermediate vessel is lignified toward the newly formed phloem group B'; x 300.

6.

7.

8.

9.
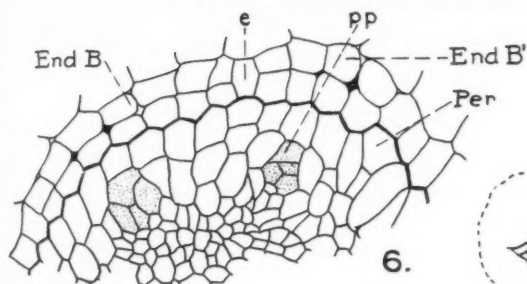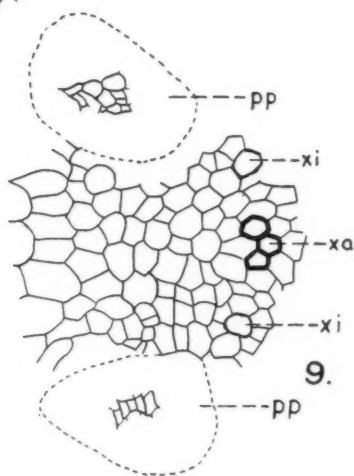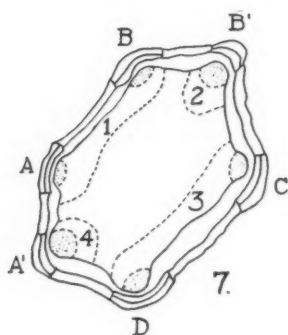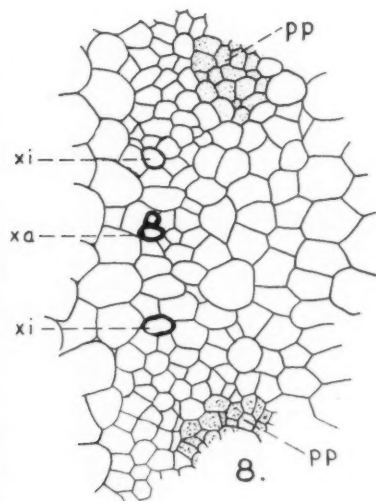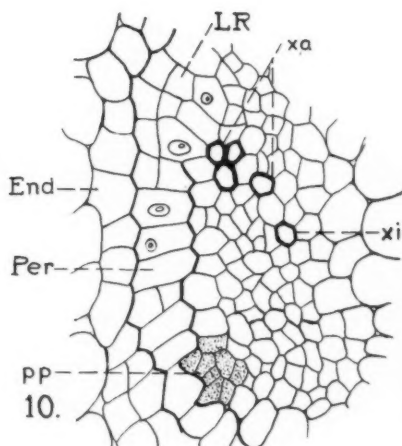
10.

PLATE III

FIGS. 11-14. Seedling 5, three days old. Completion of transition in intercotyledonary xylem group 4 and phloem B'. Figs. 10-14 are at intervals of .14 mm., .19 mm., .33 mm., and .93 mm. respectively; x 300.

11.

12

13.

14.
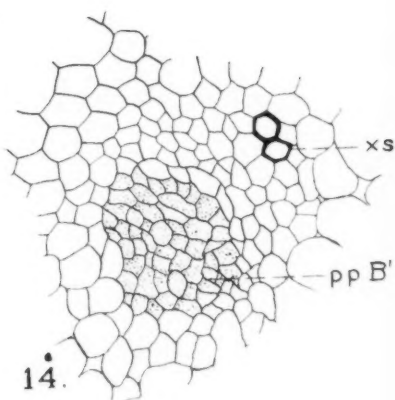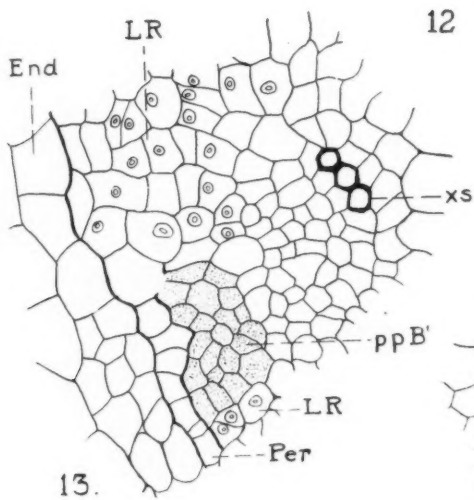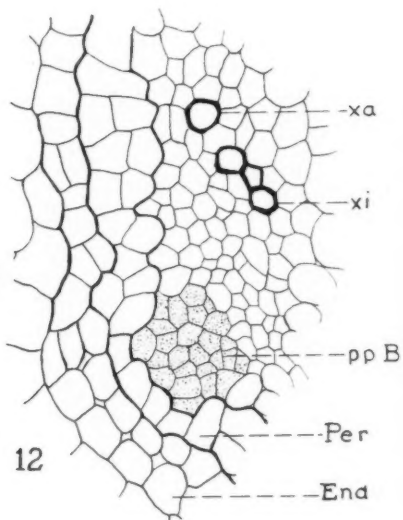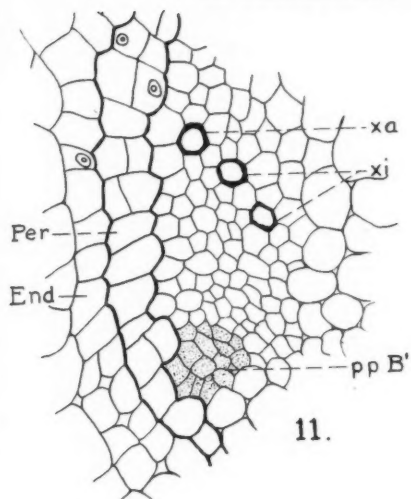
PLATE IV

FIGS. 15 AND 16.   Seedling 5, three days old.

FIG. 15.   "Double" midrib bundle at base of cotyledon; x 300.

FIG. 16.   Midrib of cotyledon 2.4 mm. from the base (1.7 mm. above Fig. 15).   The bundle is composed of all superposed xylem and one phloem group; x 300.

FIGS. 17-19.   Seedling 13, five days old.

FIG. 17.   Diagram of young root; x 72.

FIG. 18.   Detail from Fig. 17.   All xylem and phloem are alternate; x 300.

FIG. 19.   Diagram of older portion of root; x 72.

xi

xa

xi

xs

15.

15.

16.

17.

18.

19.
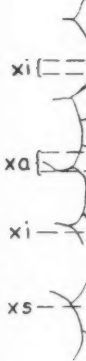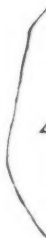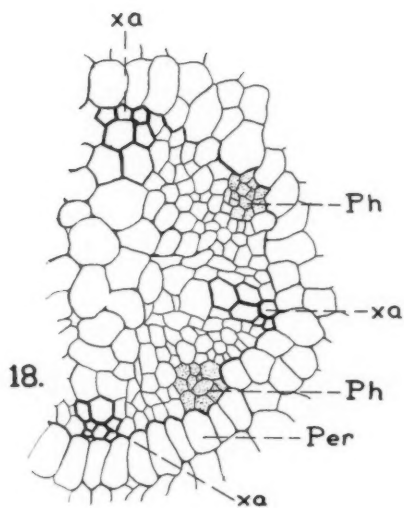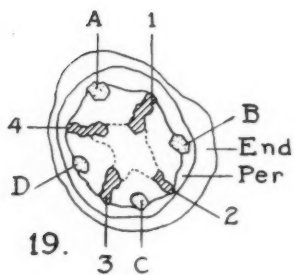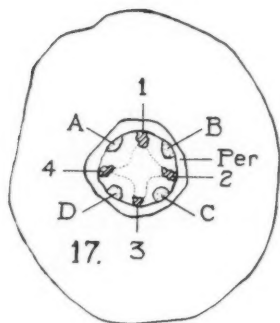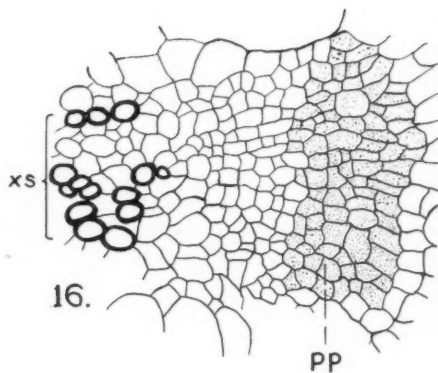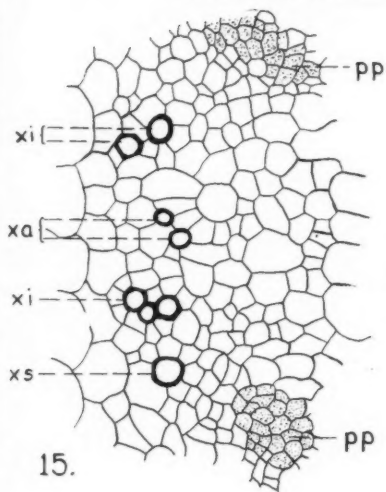
PLATE V

FIGS. 20-22.   Seedling 13, five days old.

FIG. 20.   Detail of two xylem groups and one phloem group of Fig. 19; x 300.

FIG. 21.   Diagram of still higher portion of root stele; x 72.

FIG. 22.   Detail from Fig. 21 showing an area comparable to Fig. 20; x 300.

Duct-

End-
Ph—

Per-
xa—

Ph —

End-
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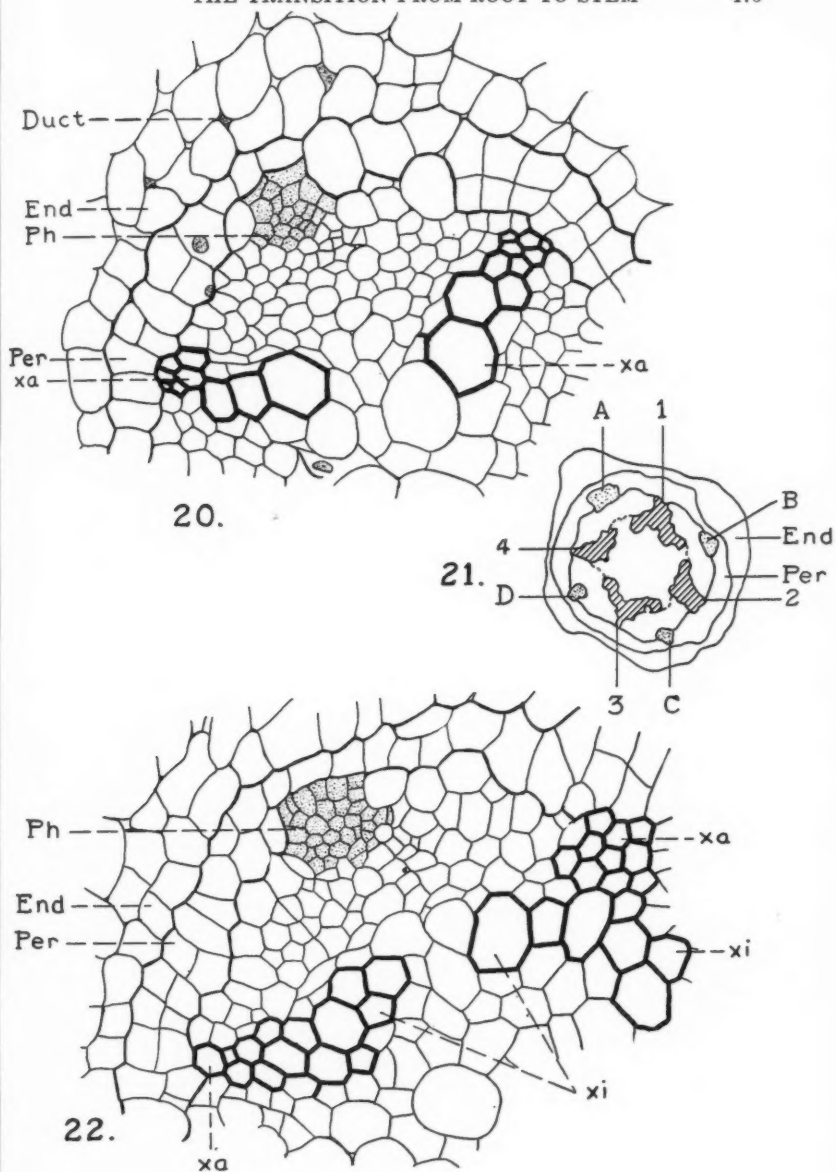
PLATE VI

FIGS. 23-26.   Seedling 13, five days old.

FIG. 23.   Diagram of stelar region at the base of the root showing the splitting of two phloem groups and the joining of three xylem groups by the formation of superposed xylem; x 72.

FIG. 24.   Detail of splitting phloem group from Fig. 23; x 300.

FIG. 25.   Diagram of stelar arrangement at the top of the hypocotyl; x 72.

FIG. 26.   Diagram of a section through the bases of the cotyledons; x 40.

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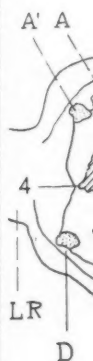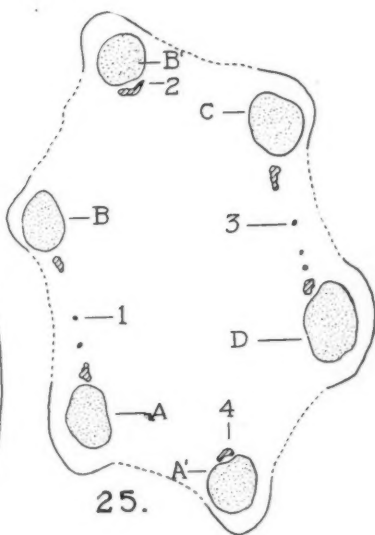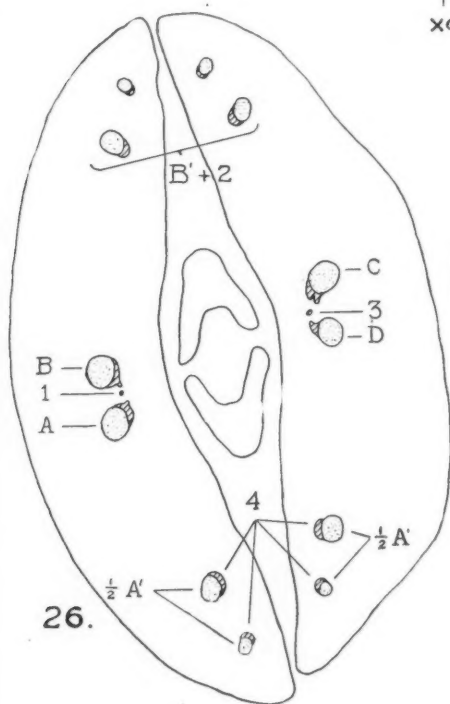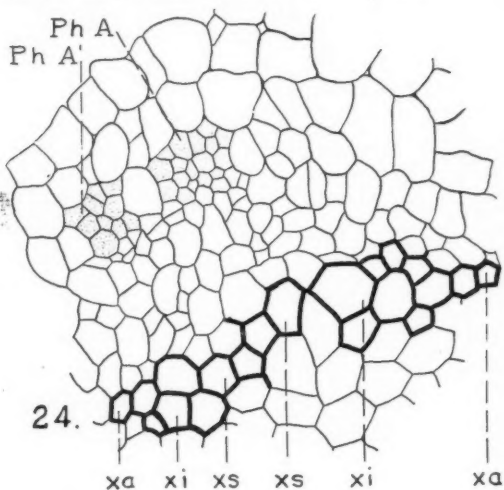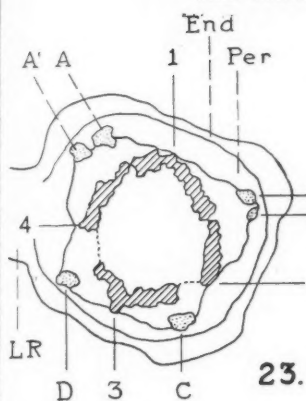
PLATE VII

FIGS. 27-29.   Seedling 13, five days old.

FIG. 27.   Diagram of stelar region at base of hypocotyl; x 72.

FIG. 28.   Detail of intercotyledonary bundle from Fig. 27; x 300.

FIG. 29.   Detail of cotyledonary bundle from Fig. 27; x 300.

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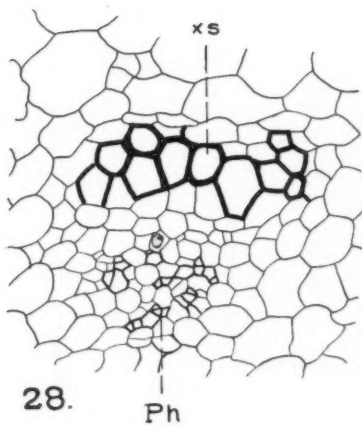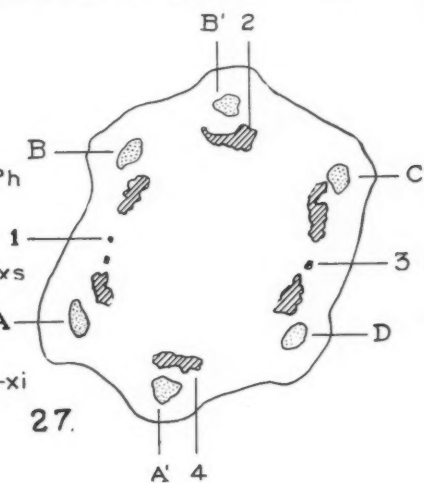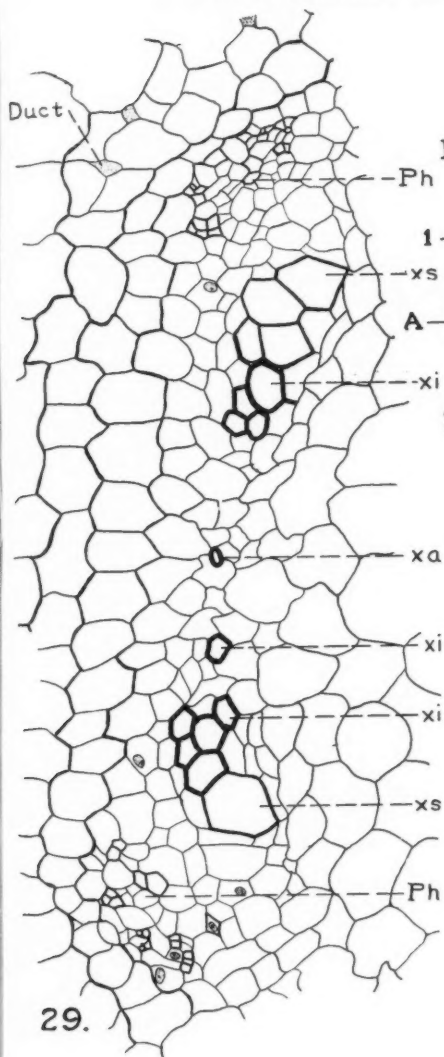
PLATE VIII

Figs. 30-32.   Seedling 13, five days old.

Fig. 30.   Midrib bundle of cotyledon near tip; x 300.

Fig. 31.   Upper epidermis (ep) of cotyledon showing stoma (st) with guard cells (g) ; x 300.

Fig. 32.   Lower epidermis of cotyledon labeled as in Fig. 31; x 300.
Figures 33-46 are of *Arctium minus.*
Figures 33-38 are of nine day old seedlings.

Fig. 33.   Diarch root stele; x 300.

Fig. 34.   Alternate xylem in stele of hypocotyl; x 300.

Fig. 35.   Detail of xylem and two adjacent phloem groups at top of hypocotyl; x 300.

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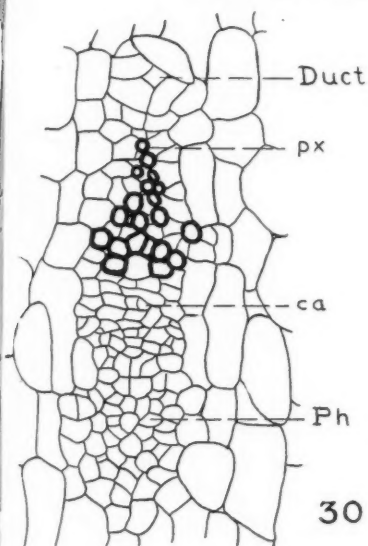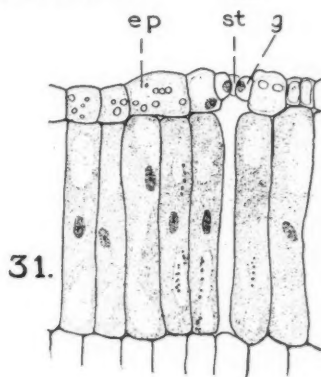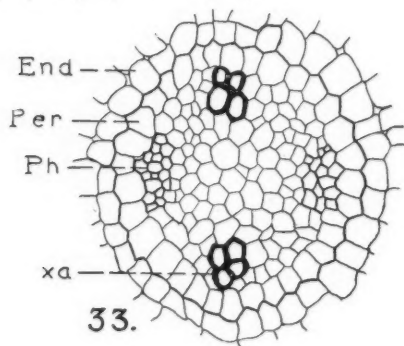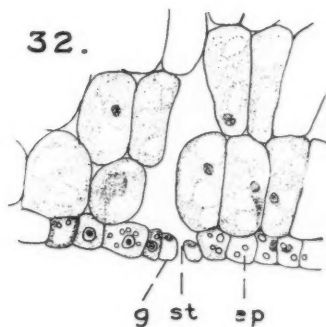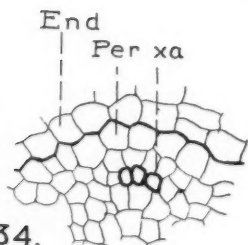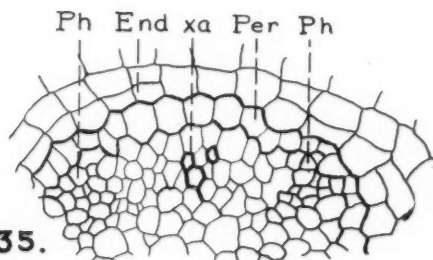
PLATE IX

FIG. 36.   Detail of "double bundle" of midrib at base of cotyledon; x 300.

FIG. 37.   Detail of midrib of cotyledon .84 mm. above Fig. 36 or 1 mm. above the top of the cotyledonary tube; x 300.

FIG. 38.   Detail of lateral bundle of cotyledon at same level as Fig. 37; x 300.

FIGS. 39-46 are of a thirteen-day seedling.

FIG. 39.   Detail of stele of root 1.5 mm. below base of hypocotyl; x 300.

FIG. 40.   Half of stele of hypocotyl showing phloem group divided into three areas; x 300.

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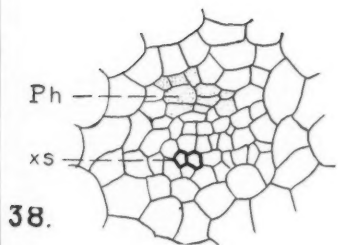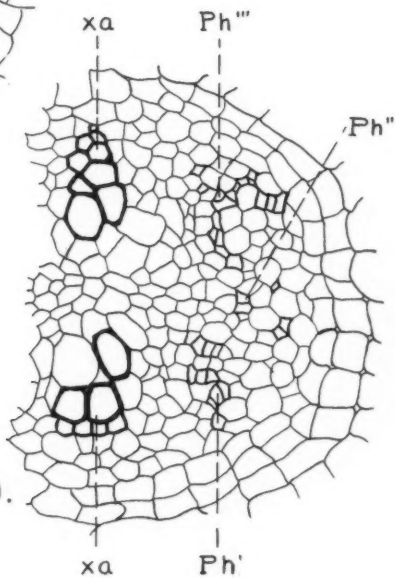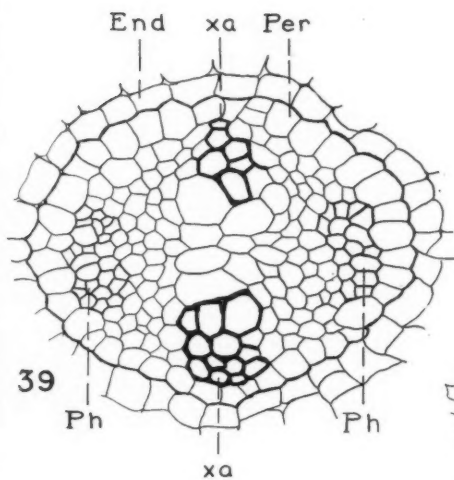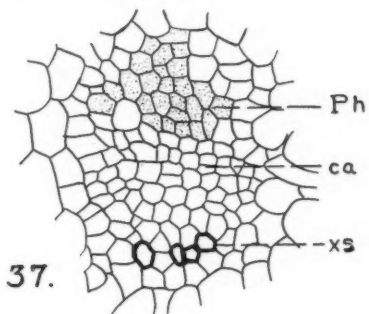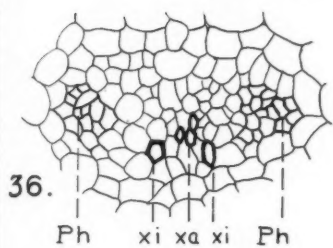
PLATE X

FIG. 41.   Half of stele of hypocotyl 2 mm. from the top, showing cotyledonary and intercotyledonary xylem groups and also the three phloem groups of one side; x 300.

FIG. 42.   Detail of cotyledonary strand in stele at top of hypocotyl; x 300.

FIG. 43.   Detail of intercotyledonary strand in stele at top of hypocotyl; x 300.

FIG. 44.   Midrib at base of cotyledon showing alternate xylem vessels being resorbed; x 300.

FIG. 45.   Cotyledon midrib 1.8 mm. above Fig. 44; x 300.

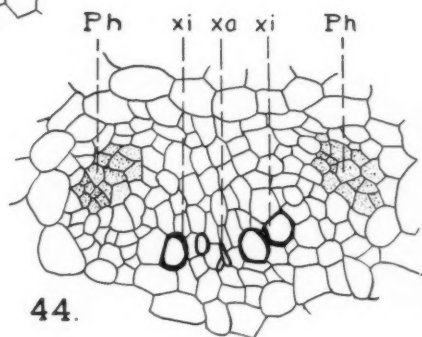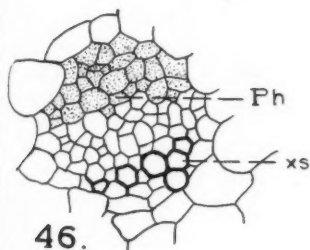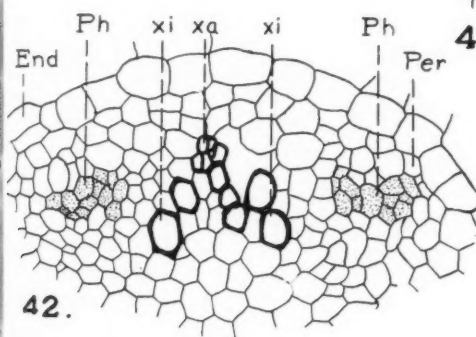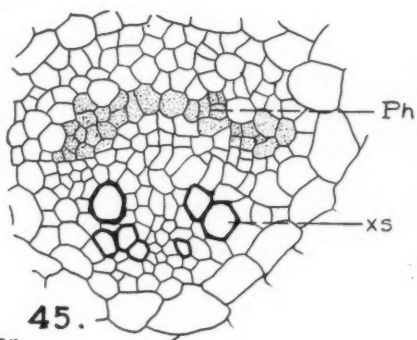FIG. 46.   Lateral bundle of cotyledon at same level as Fig. 45; x 300.

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x 300.
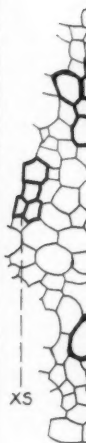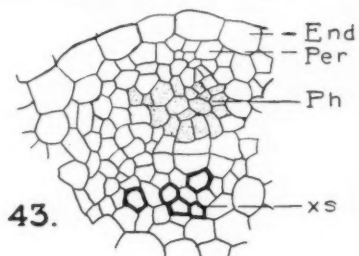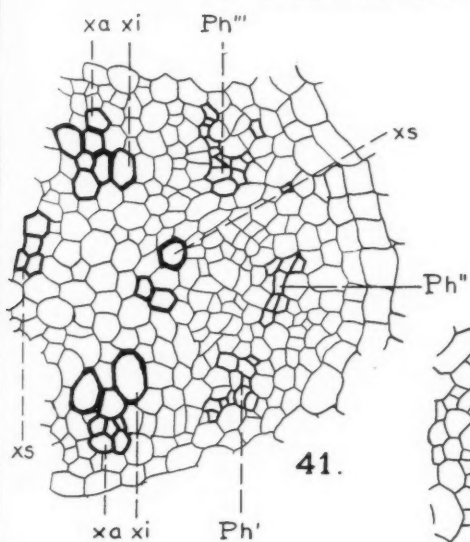
PLATE XI

FIG. 47.   Diagram of vascular transition in *Helianthus annuus*.
FIG. 48.   Diagram of vascular transition in *Arctium minus*.

d. Cotyledons

c. Hypocotyl

b. Transition

a. Root

47. Helianthus annuus
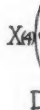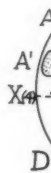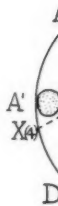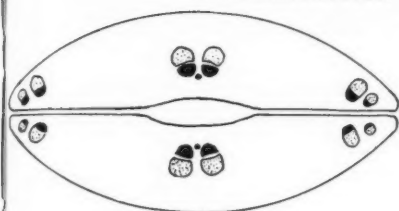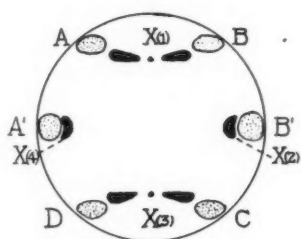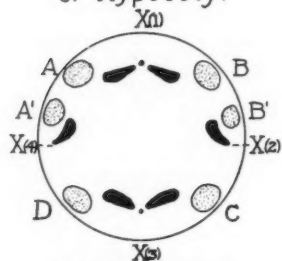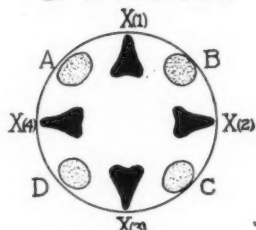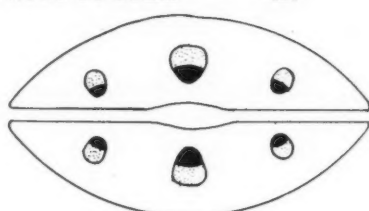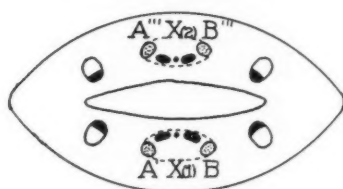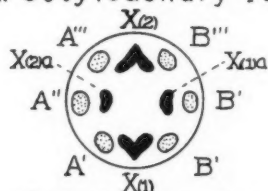
e. Cotyledons

d. Cotyledonary Tube

c. Top of Hypocotyl
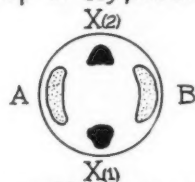
b. Hypocotyl

a. Root

48. Arctium minus

SHEPARD'S GREENE COUNTY FLORA

An Unpublished List of Plants of Greene County, Missouri, by Prof. Edward M. Shepard, Springfield, Missouri.

BENJAMIN FRANKLIN BUSH

Sometime during the year 1883, Prof. Shepard, President of Drury College, Springfield, Missouri, made a list of the plants, either known to him from, or collected in, Greene County, Missouri, which he very kindly sent to me to be used in a Flora of Missouri, which I then had in contemplation.

This list has never been published, and I now present it, with some notes on the species which Shepard has on his list. This is not a very long list of species, but it contains the names of some species that are very interesting and noteworthy, and on these I have ventured to make some notations. It will be seen that there are many gaps and omissions in this list, mostly of the more common and abundant species, which leads one to assume that Shepard did not attempt to collect, or make notes on, those species. It is also plainly apparent that he did not attempt to collect the carices and grasses, only one species each of these large families is listed, showing that he was not attracted by this group.

I am prompted to publish this short list of Greene County plants, that some one more fully prepared will be induced to publish a supplemental list, bringing the list up to date.

1. *Clematis Viorna* L.

    I assume Shepard must have had in mind the species we now know as *C. versicolor* Small, a species not yet described when he made his list.

2. *Anemone cylindrica* A. Gray.

3. *Anemone caroliniana* Walt.

4. *Anemone decapetala* Ard.

    No doubt the same as the last-mentioned species, as it then was commonly mistaken for *A. decapetala*.

5. *Thalictrum anemonoides* Michx.

6. *Thalictrum purpurascens* L.
   Probably what is now considered to be *T. revolutum* DC., a species not recognized at the time Shepard prepared his list.

7. *Ranunculus rhomboideus* Goldie.
   It seems to me very improbable that this high plains and prairie species should be found in Greene County, and I have not seen it from Missouri.

8. *Actaea alba* Bigel.

9. *Hydrastis canadensis* L.

10. *Caulophyllum thalictroides* Michx.

11. *Nuphar advena* Ait.

12. *Selenia aurea* Nutt.
    Common to all the White River region in the Ozarks.

13. *Cardamine rotundifolia* Michx.

14. *Arabis patens* Sulliv.

15. *Draba cuneifolia* Nutt.

16. *Nasturtium lacustre* A. Gray.
    I am unable to guess what species Shepard had in mind when he put this name down in his list, but it surely could not have been *N. lacustre,* as that species is unknown to be a Missouri species.

17. *Nasturtium palustre* DC.

18. *Helianthemum canadense* Michx.
    Probably the species we know as *H. majus,* as *H. canadense* is unknown to me for Missouri.

19. *Lechea major* Michx.
    The common species of the Ozark region.

20. *Lechea minor* Lam.
    Undoubtedly the same as the next following species, as *L. minor* is not known for Missouri.

21. *Lechea tenuifolia* Lam.

22. *Viola sagittata* Ait.

23. *Viola pedata* L.

24. *Viola pedata bicolor* Pursh.

25. *Viola cucullata palmata* A. Gray.
    Certainly not the species of New England, and most probably what we now know as *V. triloba* Schwein.

26. *Viola striata* Ait.

27. *Silene regia* Sims.

28. *Arenaria stricta* Michx.

29. *Cerastium nutans* Raf.

30. *Talinum teretifolium* Pursh.
    No doubt the species we now know as *T. calycinum.*

31. *Claytonia caroliniana* Michx.
    Shepard evidently mistook the common *C. virginica* for this species, which has not been found in Missouri.

32. *Ascyrum Crux-Andreae* L.

33. *Hypericum canadense* L.
    I feel certain that this must be *H. Drummondii*, which is common in the Ozark region, and not *H. canadense* of the eastern states.

34. *Hypericum mutilum* L.

35. *Hypericum nudiflorum* Michx.
    Certainly not the *H. nudiflorum* of the southeastern States, and very probably *H. cistifolium*, which is often erroneously determined as *H. nudiflorum.*

36. *Hypericum Sarothra* Michx.

37. *Linum virginianum* L.

38. *Geranium Robertianum* L.
    Probably only *G. carolinianum*, as no specimens are known of *G. Robertianum* from Missouri.

39. *Ptelea trifoliata* L.

40. *Rhus venenata* DC.
    I am unable to fix the identity of this, and it is quite clear that *R. venenata* does not occur in the State. Perhaps based on some specimen of *R. typhina*, which is commonly cultivated in Missouri.

41. *Polygala incarnata* L.
42. *Polygala Senega* L.
43. *Polygala Senega latifolia* T. & G.
44. *Polygala sanguinea* L.
45. *Polygala verticillata* L.
46. *Baptisia leucophaea* Nutt.
47. *Trifolium repens* L.
48. *Trifolium reflexum* L.
49. *Tephrosia virginiana* Pers.
50. *Astragalus mexicanus* A. DC.
51. *Astragalus distortus* T. & G.
52. *Astragalus plattensis* Nutt.
53. *Desmodium ciliare* DC.
54. *Desmodium nudiflorum* DC.
55. *Desmodium pauciflorum* DC.

   Not at all likely that this is the species of the lowlands of Southeastern Missouri, and I am unable to guess what species Shepard had in mind when he wrote this in his list.

56. *Desmodium tenuifolium* T. & G.

   Probably only a narrow-leaved form of *D. bracteosum*.

57. *Stylosanthes elatior* Swartz.
58. *Vicia caroliniana* Walt.
59. *Cassia nictitans* L.
60. *Prunus serotina* Ehrh.
61. *Spiraea salicifolia* L.

   I have much doubt about the identity of this, as *S. salicifolia* has been found in Missouri only in the northern half.

62. *Gillenia stipulacea* Nutt.
63. *Fragaria vesca* L.

   The European species has not been found introduced in any part of the State, and I assume that Shepard must have had *F. illinoensis* in hand when he identified his specimens.

64. *Potentilla argentea* L.
    This European Cinquefoil has not been found in Missouri, so far as I now know.

65. *Potentilla canadensis simplex* T. & G.
    It is very doubtful if this is really *P. simplex*, as we have no knowledge of its occurrence in the State.

66. *Amelanchier canadensis oblongifolia* A. Gray.
    As now recognized this form does not occur in the State, and the specimens Shepard identified as this must belong to *A. canadensis*, the common form in Missouri.

67. *Heuchera hispida* Pursh.

68. *Hydrangea radiata* Walt.
    Shepard has evidently made an erroneous determination in this case, as nothing is known of this species in Missouri.

69. *Sedum stenopetalum* Pursh.
    No doubt this is the species formerly known under the name *S. Torreyi*, as *S. stenopetalum* does not occur in Missouri.

70. *Callitriche heterophylla* Pursh.

71. *Oenothera missouriensis* Sims.

72. *Passiflora lutea* L.

73. *Opuntia Rafinesquii* Engelm.

74. *Archangelica hirsuta* T. & G.

75. *Archemora rigida* DC.

76. *Thaspium aureum* Nutt.

77. *Thaspium barbinode* Nutt.

78. *Thaspium trifoliatum atropurpureum* T. & G.

79. *Cicuta maculata* L.

80. *Osmorrhiza longistylis* DC.

81. *Erigenia bulbosa* Nutt.

82. *Eryngium yuccaefolium* Michx.

83. *Sanicula marilandica* L.

84. *Aralia quinquefolia* L.

85. *Cornus florida* L.
86. *Viburnum prunifolium* L.
87. *Houstonia purpurea* L.
88. *Houstonia purpurea ciliolata* A. Gray.
    Probably only *H. longifolia*, which is common in the Ozark region.
89. *Oldenlandia glomerata* Michx.
    I suspect that Shepard must have had specimens of *Spermacoce glabra*, and made an erroneous determination.
90. *Diodia teres* Walt.
91. *Dipsacus sylvestris* Huds.
92. *Conoclinium coelestinum* DC.
93. *Solidago rigida* L.
94. *Solidago tenuifolia* Pursh.
95. *Solidago petiolaris* Ait.
96. *Aster patens* Ait.
97. *Aster sagittifolius* Willd.
98. *Aster aestivus* A. Gray.
    I am unable to decide what Shepard had in hand when he put this in his list.
99. *Erigeron divaricatum* Michx.
100. *Erigeron bellidastrum* Muhl.
101. *Polymnia canadensis* L.
102. *Silphium terebinthinaceum* L.
103. *Parthenium integrifolium* L.
104. *Ambrosia bidentata* Michx.
105. *Echinacea purpurea* Moench.
106. *Actinomeris helianthoides* Nutt.
107. *Coreopsis palmata* Nutt.
108. *Coreopsis auriculata* L.
109. *Krigia virginica* Willd.
110. *Sonchus asper* Vill.
111. *Prenanthes racemosa* Michx.
112. *Hieracium longipilum* Torr.
113. *Pyrrhopappus carolinianus* DC.

114. *Cirsium discolor* Spreng.
     I feel sure this is only *C. altissimum*, which Shepard
     must have overlooked.

115. *Cirsium virginianum* Michx.
     No doubt the same as the last mentioned, as this species
     is not known so far west as Greene County.

116. *Lobelia cardinalis* L.

117. *Lobelia spicata* Lam.

118. *Vaccinium corymbosum* L.
     Shepard must have misidentified specimens of *V. vacil-
     lans* for this as no collection is known of this species
     from Missouri.

119. *Monotropa uniflora* L.

120. *Steironema longifolium* A. Gray.

121. *Steironema lanceolatum* A. Gray.

122. *Dodecatheon Meadia* L.

123. *Amsonia Tabernaemontana* Walt.
     I am unable to guess what species Shepard had in mind,
     but it evidently was not Walter's species.

124. *Apocynum androsaemifolium* L.

125. *Asclepias quadrifolia* Jacq.

126. *Acerates longifolia* Ell.

127. *Gonolobus laevis macrophyllus* Michx.
     Possibly this species, but as there are several other
     species that are more or less common in southern Mis-
     souri, it is somewhat doubtful if correctly identified.

128. *Sabbatia angularis* Pursh.

129. *Cynoglossum Morisoni* DC.

130. *Polemonium reptans* L.

131. *Phlox paniculata* L.

132. *Phlox maculata* L.
     Probably only *P. divaricata*, which is the common
     species in the State, *P. maculata* not being known to
     me as a Missouri species.

133. *Phlox divaricata* L.

134. *Phlox procumbens* Lehm.

    No doubt the same as *P. pilosa*, which is common in the State, and which Shepard does not list.

135. *Phlox amoena* Sims.

    Evidently the same as *P. pilosa*, which is often determined as *P. amoena* by collectors, but which has not yet been found in the State.

136. *Phacelia parviflora* Pursh.

137. *Phacelia parviflora hirsuta* A. Gray.

138. *Ipomoea Quamoclit* L.

139. *Convolvulus spithamaeus* L.

140. *Cuscuta arvensis* Beyrich.

141. *Pentstemon gracilis* Nutt.

142. *Mimulus Jamesii* Torr.

    I have no idea what Shepard collected, and I doubt very much if his specimens were this species, which I have never seen from the State.

143. *Veronica Anagallis* L.

144. *Buchnera Americana* L.

145. *Gerardia grandiflora* Benth.

146. *Gerardia pedicularia* L.

    This is probably the same as *G. pectinata*, which is more or less common in sandstone barrens in the Ozark region.

147. *Pedicularis lanceolata* Michx.

    Shepard evidently found *P. canadensis*, and determined it as *P. lanceolata*, a species that has not so far as I now know been found in Missouri.

148. *Castilleia coccinea* Spreng.

149. *Castilleia sessiliflora* Pursh.

    Evidently an error of determination on the part of Shepard, as this plant is known in Missouri only from the terraced mounds in the extreme northwestern part.

150. *Aphyllon uniflorum* T. & G.

151. *Tecoma radicans* Juss.

152. *Ruellia strepens* L.

153. *Dianthera americana* L.

154. *Lycopus rubellus* Moench.
155. *Lycopus europaeus sinuatus* A. Gray.
156. *Pycnanthemum lanceolatum* Pursh.
157. *Pycnanthemum leptodon* A. Gray.
     I cannot be sure that this is what Shepard collected, as I have never seen any specimens of *P. leptodon* from the State.
158. *Calamintha Nuttallii* A. Gray.
159. *Monarda punctata* L.
160. *Plantago sparsiflora* Michx.
     Undoubtely an error of identification on the part of Shepard, as this species is not known to occur in Missouri, or in the Manual range, even.
161. *Plantago cordata* Lam.
162. *Plantago Rugelii* Decaisne.
163. *Plantago pusilla* Nutt.
164. *Chenopodium urbicum* L.
165. *Rumex britannica* L.
166. *Polygonum tenue* Michx.
167. *Polygonum arifolium* L.
     I feel very doubtful that this species has been found in Greene County, and believe that Shepard must have found *P. sagittatum*, and erroneously determined it as *P. arifolium*.
168. *Aristolochia tomentosa* Sims.
169. *Sassafras officinale* Nees.
170. *Lindera Benzoin* Blume.
171. *Lindera melissaefolium* Blume.
     No doubt a mistake in determination by Shepard as this species does not occur in Missouri, nor in the Manual range, so far as is now known.
172. *Comandra umbellata* Nutt.
173. *Croton glandulosus* L.
174. *Tragia urticaefolia* Michx.

175. *Acalypha caroliniana* Ell.

   I think Shepard must have had *A. virginica* in hand when he made this determination, as he does not list this species.

176. *Acalypha virginica gracilens* Muell.

177. *Juglans cinerea* L.

178. *Salix discolor* Muhl.

   I am unable to guess what species Shepard had specimens of, but I feel sure they were not *S. discolor*, which is known in Missouri only in the extreme northeastern part.

179. *Salix humilis* Marsh.

180. *Juniperus communis* L.

   Shepard most certainly made an error in the determination of his specimen, as this species is not known to occur in Missouri.

181. *Liparis liliifolia* Richard.

182. *Calopogon pulchellus* R. Br.

183. *Orchis spectabilis* L.

184. *Cypripedium candidum* Muhl.

185. *Cypripedium parviflorum* Salisb.

186. *Cypripedium pubescens* Willd.

187. *Melanthium virginicum* L.

188. *Trillium sessile* L.

189. *Allium striatum* Jacq.

190. *Smilax hispida* Muhl.

191. *Commelina virginica* L.

192. *Tradescantia rosea* Vent.

   I have no doubt that some other species of *Tradescantia* was collected by Shepard, probably *T. brevicaulis*, as no specimens of *T. rosea* have been seen from Missouri.

193. *Xyris flexuosa* Muhl.

194. *Sparganium simplex androcladum* Engelm.

195. *Sagittaria calycina* Engelm.

196. *Carex virescens* Muhl.

197. *Alopecurus pratensis* L.

    I do not know what species of grass Shepard had in mind when he put this on his list, but I feel that he must have made an erroneous determination.

198. *Equisetum sylvaticum* L.

    Shepard's specimens must certainly have been some form of *E. arvense* and not *E. sylvaticum* which is not known for Missouri.

199. *Equisetum hyemale* L.

    Shepard's specimens most certainly were *E. laevigatum*, the common evergreen species of Missouri. *E. hyemale* has not been found in Missouri so far as known.

200. *Adiantum Capillus-Veneris* L.

201. *Asplenium pinnatifidum* Nutt.

202. *Asplenium ebeneum* Ait.

203. *Pteris aquilinum* L.

204. *Cheilanthes vestita* Sw.

205. *Cystopteris bulbifera* Bernh.

Courtney, Missouri.

THE SUGAR MAPLES

BENJAMIN FRANKLIN BUSH

For several years it has been apparent to me that the Eastern Sugar Maple has no name.

By this statement I mean the tree of New England, with the leaves green on both sides and rather soft in texture, the Sugar Tree of the nurseries, the one so much planted on lawns and along streets in the smaller cities and towns in the West, which has been called *A. saccharum*[1], *A. barbatum*[2] and *A. saccharophorum*[3].

Marshall, in his Arbustum Americanum in 1785, described four species of *Acer*, all taken from Linnaeus' Species Plantarum, of which one was given as *Acer saccharum*, which has generally been accepted as supposedly for the Eastern Sugar Maple, but there is no doubt that he intended this name for the Silver Maple.

Marshall's name was adopted for the Eastern Sugar Maple, first by Trelease in 1894, accepted by Engler in 1902, Robinson and Fernald in 1908, Schneider in 1909, Britton & Brown in 1913, Bean in 1921, Sargent in 1922, Rehder in 1927 and Sudworth in 1927, but, notwithstanding this long array of names of writers above to the contrary, the fact remains that Marshall never intended to name or describe any species of Sugar Maple.

Marshall's name *saccharum* can not be used for any species of Sugar Maple, for several good reasons, as follows: Marshall did not intend to describe a new species of *Acer* when he wrote *Acer saccharum*, but unquestionably followed Linnaeus' Species Plantarum[4], the species of which he accepted for his Arbustum[5]; his name *saccharum* is taken directly from Lin-

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[1] *Acer saccharum* Marshall, Arb. Amer. 4: 1785, being a misprint for *Acer saccharinum* Linnaeus, 1055. 1753.

[2] *Acer barbatum* Michx. Fl. Am. 2: 252, 1803.

[3] *Acer saccharophorum* K. Koch, Hort. Dendrol. 80. 1853.

[4] Species Plantarum, 1055. 1753.

[5] Arbustum Americanum, 4: 1785.

naeus, but either he left out the letters *in* in preparing his Ms. for the printer, or the printer inadvertently omitted them, which made Marshall's name read *Acer saccharum,* instead of *A. saccharinum,* as is found in Linnaeus' Spec. Pl.; Marshall's description of *A. saccharum* was taken from *A. saccharinum* Linnaeus, the Silver Maple, and his description fits that species quite clearly, but does not fit any species of Sugar Maple, *A. barbatum glaucum*[6], *A. nigrum*[7] or what is here proposed as the Eastern Sugar Maple.

Mr. T. A. Sprague has quite recently[8] attempted to prove that Marshall described a new species of *Acer* under the name of *A. saccharum,* which he claims is the botanical name of the Sugar Maple, but does not indicate which species he is attempting to fasten Marshall's name *saccharum* upon. Mr. Sprague has taken exception to some observations made by Mr. Mackenzie on Marshall's name, which I will refer to at some length later on in this paper.

In 1788, Lézermes published in Paris a French translation of Marshall's Arbustum[9], in which Marshall's name *saccharum* is given as *A. saccharinum,* and there is nothing in this translation to warrant Mr. Sprague's assumption that Marshall did not authorize the correction.

But whether Marshall authorized Lézermes to correct his name *saccharum* to *saccharinum,* or not, does not have any bearing on the legitimacy of the name itself, which is the contention I make, and this translation shows conclusively that Lézermes recognized the fact that Marshall intended to use the name *saccharinum,* and that name for the Silver Maple.

Mr. Sprague, in the paper mentioned above, has attempted to legitimize Marshall's fictitious name *saccharum* for the Sugar Maple, without going back to the beginning and ascertaining just what Marshall had in mind and described under this name.

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[6] Bush, Am. Midland Nat. **11**: 116. 1928.
[7] Michaux. f. Hist. Arb. Am. **2**: 238. 1810.
[8] Kew Bull. Misc. Inform. 81-82. 1929.
[9] Cat. Alphabetique des Arbres et Arbrisseaux, 1788.

I have examined Marshall's description carefully and there is not a single paragraph in it that describes any Sugar Maple, but his description applies quite clearly to the Silver Maple, the *A. saccharinum* of Linnaeus, the species he had in mind at the time, no species of Sugar Maple being known to Linnaeus and down to Marshall's time.

Mr. K. K. Mackenzie in a short note[10], shows that the fictitious name *saccharum* of Marshall should be abandoned, as it was a misprint of Linnaeus' *saccharinum*, and that Marshall did not here describe any Sugar Maple or any new species of *Acer*, none being known to him; but Mr. Mackenzie does not indicate in this note what name Marshall's supposedly new species should bear. The main point in Mr. Mackenzie's note is his statement "the name '*Acer saccharum*' does, it is true, appear as cited, but this was merely a typographical error for *Acer saccharinum* L."

Mr. Mackenzie has further shown[11] that Marshall intended to describe the four species known and described by Linnaeus, *A. rubrum, saccharinum, Pennsylvanicum* and *Negundo*, in his Arbustum, and that neither Linnaeus or Marshall ever described any species of Sugar Maple.

Michaux's name *A. barbatum* can not be used for any species of Sugar Maple, as his description was based mostly on *A. rubrum*, and his type-specimen is a leafing branch of that species, and a flowering sheet of *A. nigrum, A. barbatum glaucum*, or some species of Sugar Maple not determined.

K. Koch[12], realizing that Michaux's species *barbatum* was not valid on account of having been described from a specimen of *A. rubrum* in great part and some from either *A. nigrum, A. barbatum glaucum*, or some other Sugar Maple, in small part, and that Marshall's *A. saccharum* was a misprint for *A. saccharinum* Linnaeus, proposed *Acer saccharophorum* to replace these names, but without description or citation of type-specimens.

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[10] Rhodora **28**: 111-112. 1926.
[11] Rhodora **28**: 233-234. 1926.
[12] Hort. Dendrol. 80. 1856.

Had Koch given a description of any species of Sugar Maple, or cited an undisputed specimen to represent his new name, his name might be taken up for one of our Sugar Maples, but in the absence of these his name becomes a *nomen nudum*.

As no other writer has given a name to the Eastern Sugar Maple, it has the unique distinction of being a well-known species without a name, therefore I offer the following:

ACER **Treleaseanum**[13] n. sp.

A. saccharum Trelease, Sargent, et Amer. Aucts., pro parte, misapplying Marshall's name *saccharum*.

Leaves green on both sides and rather soft in texture.

Newfoundland and Nova Scotia to Pennsylvania and New York.

The Western Sugar Maple of the Central and Western States, having the leaves rather firm and very glaucous beneath, does not appear to ever had a specific name.

The synonymy of this species is as follows:

Acer saccharinum glaucum Pax, Engler Bot. Jahrb. 7: 242. 1886.

A. palmifolium glaucum (Pax) Schwerin. Gartenflora 42: 455. 1893.

A. saccharum glaucum (Pax) Sargent, Bot. Gaz. 67: 233. 1919.

A. barbatum glaucum (Pax) Bush, Am. Midland Nat. 11: 116. 1928.

For this species I propose the following:
ACER **subglaucum** n. sp.

Western New York, Pennsylvania to Minnesota, Ohio, Iowa and Western Missouri.

Some of the forms of this species look very distinct, at

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[13] William Trelease, b. 1856, Emeritus Professor, University of Illinois, 1926, Director of the Mo. Bot. Garden, 1889-1912, who wrote on the Sugar Maples in 1894.

least enough so to warrant their rank as varieties, of which I present the following:

ACER SUBGLAUCUM **Rugelii** (Pax) n. comb.

A. Rugelii Pax, Engler Bot. Jahr. 7: 243, 1886.

A. saccharinum Rugelii (Pax) Wesmael, Bull. Soc. Bot. Belg. 29: 61, 1890.

A. saccharum Rugelii (Pax) Rehder, Cycl. Am. Hort. 1: 13, 1900.

A barbatum Rugelii (Pax) Bush, Am. Midland Nat. 11: 116, 1928.

This is the rather medium-sized tree with firm smooth leaves, of rocky or flinty hills, in southern Missouri, northern Arkansas, eastern Kansas and eastern Oklahoma. Sometimes appearing very distinct from *A. subglaucum,* and still more so does the following:

ACER SUBGLAUCUM **Schneckii** (Rehder) n. comb.

A. saccharum Schneckii Rehder, Sargent, Trees and Shrubs 2: 256. 1913.

A. barbatum Schneckii (Rehder) Bush, Am. Midland Nat. 11: 116, 1928.

This is the large tree of Western Illinois, Eastern Missouri and Northeastern Arkansas, with large leaves having the petioles and lower surface of the leaves densely brownish-tomentose.

The relationship of the next-following is somewhat doubtful, but I offer for it the following:

ACER SUBGLAUCUM **sinuosum** (Rehder) n. comb.

A. sinuosum Rehder, Sargent, Trees and Shrubs 2: 255, 1913.

A. saccharum sinuosum (Rehder) Sargent, Bot. Gaz. 67: 234. 1919.

Courtney, Missouri.

N O T E

"The Auk," Vol. XLVIII., No. 3, comments on the poisoning operations directed against predatory mammals and rodents by the Biological Survey in the West. Reference is made to two articles setting forth authoritative data regarding the results of wide use of poison (thallium) in an effort to kill ground squirrels. These operations have been carried on in the course of the last four years to such an extent that about 50,000,000 birds and mammals (exclusive of ground squirrels) have been killed. The area covered by the operations is 5,000,000 acres, and practically half a million pounds of thallium poisoned grain was used in the year 1929. The amount is less than that used in the preceding year. Several attempts, unsuccessful thus far, have been made to prevent the future use of poison by the Biological Survey. Many individuals, societies and other institutions are doing their best to bring this matter before the public in order to arouse general concerted action which would put an end to such destructive operations and preserve whatever of wild life there is left in the country.

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